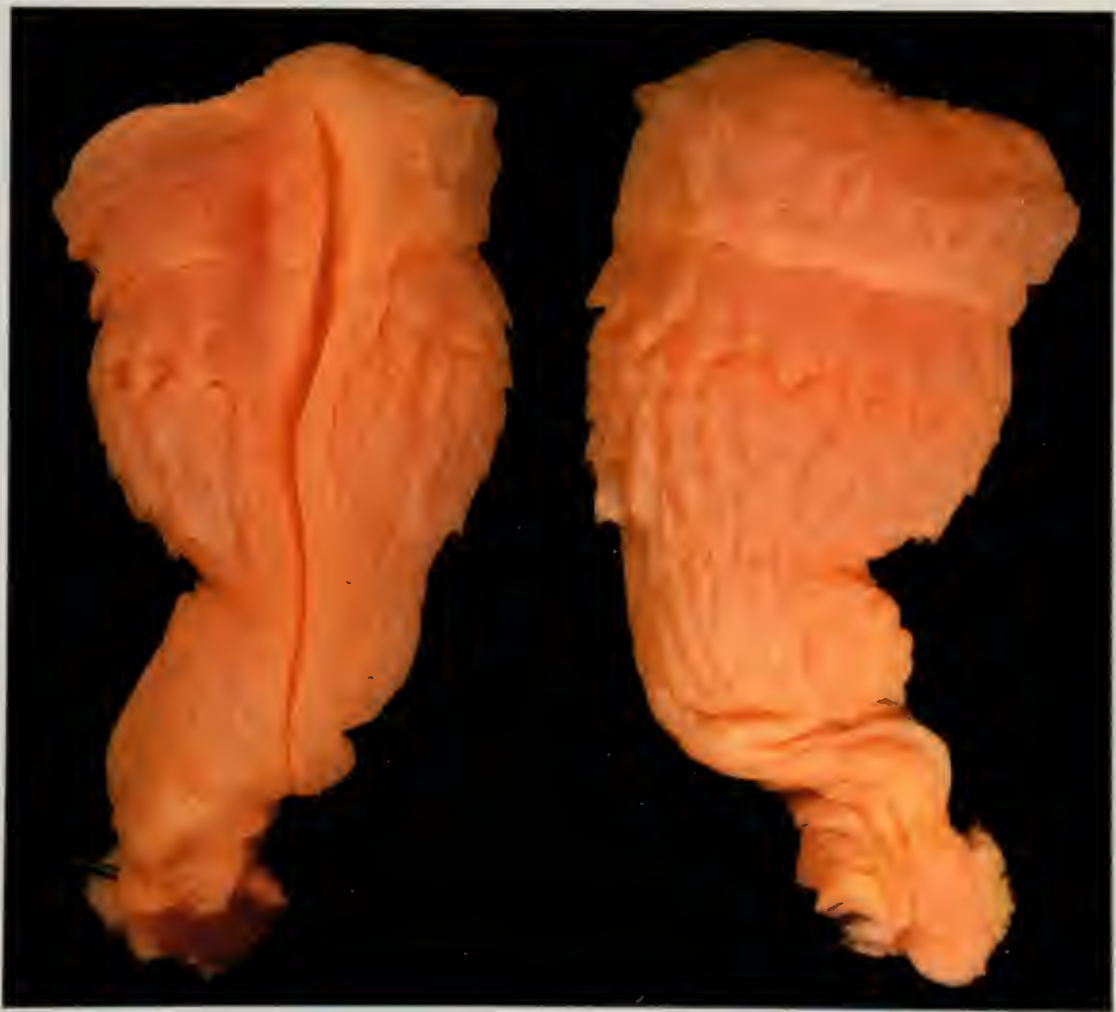# Systematics of the Neotropical Snake *Dendrophidion paucicarinatum* (COPE), with a Description of Its Hemipenis (Serpentes: Colubridae)

JOHN E. CADLE AND JAY M. SAVAGE

SYSTEMATICS OF THE NEOTROPICAL SNAKE *DENDROPHIDION PAUCICARINATUM* (COPE), WITH A DESCRIPTION OF ITS HEMIPENIS (SERPENTES: COLUBRIDAE)

JOHN E. CADLE[1] AND JAY M. SAVAGE[2]

CONTENTS

ABSTRACT. We present the first modern comprehensive systematic treatment of the Central American snake *Dendrophidion paucicarinatum* (Cope). We redescribe the species on the basis of a large sample from throughout its range, redescribe and illustrate the holotype, and provide a detailed treatment of its hemipenial morphology. *Dendrophidion paucicarinatum* is distinguished from other species of the genus by a combination of having more ventrals (>175), fewer subcaudals (<140), very weak keels on the dorsal scales, and distinct transverse dark lines across each ventral in adults. It is an upland species found almost exclusively above 1,000 m in mountainous regions of Costa Rica and western Panama, primarily in premontane and montane humid to wet forests and cloud forests. It is a large species attaining a total length of 1.5 m and is diurnal and anurophagous like other species of *Dendrophidion*. Known clutch sizes are 3–12. Evidence from the Monteverde region in Costa Rica suggests that populations of *D. paucicarinatum* declined after collapse of the frog fauna due to epidemic disease (chytridiomycosis). The hemipenis of *D. paucicarinatum* is similar to those of most other species of *Dendrophidion* in having reduced calycular structures and a largely nude apex; the sulcus spermaticus is centrolineal and undivided. The spinose region is delimited distally by a uniform row of distinctly enlarged spines, which is a character shared with *D. dendrophis* (*sensu lato*) and three species of the *D. nuchale* species complex, although these species are not thought to be closely related to *D. paucicarinatum*.

Key words: Costa Rica, Panama, systematics, Central America, *Dendrophidion*, snakes, hemipenis, morphology

RESUMEN. Presentamos el primer estudio sistemático moderno de la serpiente centroamericana *Dendrophidion paucicarinatum* (Cope). Describimos de nuevo la especie en base de muchos ejemplares desde toda la distribución, redescribimos y ilustramos el holotipo, y proveemos una descripción detallada de la morfología del hemipene. *Dendrophidion paucicarinatum* es una especie de tierras altas encontrada casi exclusivamente arriba de 1,000 m de elevación en las regiones montañosas de Costa Rica y Panamá occidental, primariamente en los bosques lluviosos premontanos y montanos y bosques nubosos. Es una especie grande que alcanza una larga total hasta 1.5 m. Es diurna y anurofaga como otras especies de *Dendrophidion*. El número de huevos por puesta es 3–12. Observaciones desde la región de Monteverde en Costa Rica sugeren que la declinación de las poblaciones de *D. paucicarinatum* resulta del desplome de la anurofauna debido a enfermedad epidémica (chitridiomicosis). El hemipene de *D. paucicarinatum* es similar a la mayoría de otras especies de *Dendrophidion* al tener estructuras calyculares reducidas y un ápice mayormente nudo; el sulco espermático es

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centrolineal y no bifurcado. La región espinosa se limita distalmente por una fila uniforme de espinas distintamente agrandadas. Este último se comparte con *D. dendrophis* (*sensu lato*) y tres especias del complejo *D. nuchale*, aunque estas especies no se piensen relacionadas cercanamente a *D. paucicarinatum*.

INTRODUCTION

Recent revisions of Central American members of the Neotropical snake genus *Dendrophidion* resulted in partition of three widespread species complexes and descriptions of five new species. Cadle (2012a) recognized three species within the *D. vinitor* complex, which now includes, in addition to the nominate species, *D. apharocybe* and *D. crybelum*. These snakes are distributed from southern Mexico to eastern Panama. Cadle (2012b) described two new South American species from western Colombia and Ecuador that had previously been confused with the primarily Central American species, *D. percarinatum*, which is known from eastern Honduras to northwestern Colombia. Cadle and Savage (2012) reviewed the *D. nuchale* complex, recognizing *D. clarkii* Dunn for snakes of this complex distributed from Costa Rica to western Colombia and Ecuador, and describing as a new species (*D. rufiterminorum*) the northern populations of the complex distributed from Belize to Costa Rica; *D. nuchale sensu stricto* is recorded only from Venezuela.

Apart from the snakes in the above three species complexes, only one other species of *Dendrophidion* is currently recognized in Central America: *D. paucicarinatum* (Cope, 1894). This species was originally described from a single Costa Rican specimen and is now known from the uplands of Costa Rica and western Panama (Lieb, 1991). After its description *D. paucicarinatum* was subsequently "forgotten" and was not mentioned in any comprehensive taxonomic works on Neotropical herpetofauna (e.g., Amaral, "1929" [1930]) until Stuart (1933) recognized its validity. Lieb (1988, 1991) and Savage (2002: 656–657) briefly summarized characteristics of *D. paucicarinatum* but there has been no formal taxonomic review of this species and its hemipenis has been described only in brief

(Savage, 2002). The color pattern and some scutellation characters of *D. paucicarinatum* are distinct from all other Central American species and it is additionally unusual in being a species primarily of upland or mountainous areas. In contrast, nearly all other Central American species are widely distributed in the lowlands (two South American species, *D. brunneum* and *D. bivittatum*, occur in the Andes and their upper elevational limits exceed that of *D. paucicarinatum*). The purpose of this paper is to summarize taxonomic characters of *D. paucicarinatum*, describe its hemipenial morphology, and make pertinent comparisons with other species of *Dendrophidion*.

MATERIALS AND METHODS

Methods for scoring dorsocaudal reductions, dorsal keeling, and aspects of color pattern are described by Cadle (2012a) for other *Dendrophidion*. Measurements are presented in millimeters. We compared linear measurements and scale counts for males and females using Student's *t* test; relative tail lengths (RTL) (tail as a proportion of snout–vent length [SVL] or total length) were compared using the Mann–Whitney *U* test. We examined retracted and everted hemipenes of *D. paucicarinatum*. The everted hemipenis described herein had been fully everted in the field. It was removed from the specimen and inflated with colored jelly as described by Myers and Cadle (2003). Hemipenial measurements (in millimeters) were taken with Helios dial calipers to the nearest 0.01 mm under a dissecting microscope. Additional comparative data on hemipenial and external morphology of other species of *Dendrophidion* are given in Cadle (2010, 2012a,b) and Cadle and Savage (2012).

Size at sexual maturity, measured as SVL, is unknown for *D. paucicarinatum*, but some other species of *Dendrophidion* mature at 400–600 mm SVL (Goldberg, 2003; Stafford, 2003; Prudente et al., 2007; see also Natural History of *Dendrophidion paucicarinatum* herein). For purposes of analyzing intraspecific differences in mean SVL of adult males and females, we analyzed the size data

Figure 1.   Holotype of *Dendrophidion paucicarinatum* (Cope) from La Candelaria, Costa Rica. AMNH R-17268. Adult female, 1,264 mm total length (841 mm SVL).

considering all specimens >400 mm SVL and separately using all specimens >500 mm SVL. Statistical results were identical and the mean adult sizes calculated for each sex differed by <20 mm; thus, we present here only the comparisons using specimens >500 mm SVL. Similarly, because RTL increases proportionally with SVL, the range of adult RTL was assessed for individuals with SVL >300 mm because RTL approaches an asymptote at approximately this size; see Klauber (1943) for an early discussion of ontogenetic growth patterns of tail proportions in snakes.

We recorded data for nearly all specimens of *D. paucicarinatum* in U.S. and Costa Rican collections, for a total of 28 males, 40 females (including the holotype), and five unsexed specimens (Appendix 1). We confirmed the identity of a few additional specimens in the Universidad de Costa Rica (UCR) collections

to augment the known localities. A gazetteer and notes on collecting localities are given in Appendix 2. Coordinates, some elevations, and other information on localities were derived primarily from Fairchild and Handley (1966; Panama), and the National Geospatial-Intelligence Agency online gazetteer (GEOnet): http://earth-info.nga.mil/gns/html. Useful geographical and historical notes on localities are Carriker (1910), Goodwin (1946), Myers (1969), and Savage (1974).

SYSTEMATICS OF *DENDROPHIDION PAUCICARINATUM* (COPE)

Figures 1–6, 8–11

Drymobius paucicarinatus Cope, 1894: 202–203 (holotype: American Museum of Natural History [AMNH] R-17268 from

"La Candelaria", Costa Rica). Cope "1894" [1895]: 427. Cope, 1895: 205. Boulenger, 1896: 626 (synonym of *Drymobius dendrophis*). Savage, 1974: 82.

Dendrophidion paucicarinatus. Stuart, 1933: 9. Slevin, 1942: 470. Dunn, 1947: 153. Taylor, 1951: 91. Smith, 1941: 73. Smith, 1958: 223. Peters and Orejas-Miranda, 1970: 80.

Dendrophidion paucicarinatum. Savage, 1973: 14; 1980: 92. Scott et al., 1983: 372. Savage and Villa, 1986: 148, 168. Lieb, 1988: 172. Villa et al., 1988: 63. Hayes et al., 1989: 50. Lieb, 1991. Ibáñez and Solís "1991" [1993]: 30, 33. Pérez-Santos et al., 1993: 116. Auth, 1994: 15. Pérez-Santos, 1999: 44, 99, 102. Pounds and Fogden, 2000: 539. Savage, 2002: 656 + pl. 417. Goldberg, 2003. Köhler, 2003: 199 + Fig. 477; 2008: 214 + Fig. 578. Solórzano, 2004: 232–234 + Figs. 57–58. Savage and Bolaños, 2009: 14. Bolaños et al., 2010 (accessed 2 February 2013).

Holotype and Type Locality. Cope (1894: 202–203) described *Drymobius paucicarinatus* from a single adult female, now AMNH R-17268 (Fig. 1), collected by Bruno Carranza from "La Candelaria" [Costa Rica]. The specimen was part of a collection from the Museo Nacional de San José sent to Cope by George K. Cherrie, who supplied Cope with specimens for several works on the herpetofauna of Costa Rica (see Myers, 1982: 23 [footnote 7] for some of the history of these collections).

On the basis of place name usage and information provided by Carriker (1910: 337, 346) and Goodwin (1946: 456), Savage (1974: 82, 102) concluded that La Candelaria is probably equivalent to "Monte Redondo," as used by ornithologists (particularly C. F. Underwood) during the late 19th and 20th centuries. It is located in San José Province south of the Candelaria (Cedral) mountain range that forms the southern rim of the Valle Central; coordinates for Monte Redondo are 09°47′17″N, 84°07′24″W (National

Geospatial-Intelligence Agency, 2013). Savage (1974: 102) gave the elevation of Monte Redondo as 1,040 m but Goodwin (1946: 456) and Carriker (1910: 346) gave its elevation as 4,000 feet (= 1,220 m) and Carriker (p. 337) further stated that "… the altitude from which specimens have come may be placed at anywhere from 4,000 to 7,000 feet" (= 1,220–2,135 m). GoogleEarth places it at about 1,170 m.

The holotype of *Dendrophidion paucicarinatum* (Fig. 1) is an adult female in fair condition; the tail is broken about 180 mm from the vent, but it is complete. There is a midventral incision in the base of the tail. The specimen is gravid, with approximately six large eggs estimated by palpation. Total length 1,264 mm; tail length 423 mm; SVL 841 mm; 182 ventrals (1 preventral); 126 subcaudals; anal plate divided; dorsocaudal reduction from 8 to 6 at subcaudal 9; dorsal scale reduction from 17 to 15 at the level of ventrals 104–105 by fusion of dorsal rows 3+4; 9/9 supralabials (2–3 touching the loreal; 4–6 touching the eye); 2/2 postoculars; 2 + 2 temporals on each side; 10/10 infralabials. The supralabial/temporal pattern, as described in Cadle (2012b: 265–266 and Fig. 1), is the *P*–pattern on both sides.

Keels are absent from dorsal scales on the neck; very weak keels are present on the 5 median rows at midbody, and very weak keels are present on all except row 1 posteriorly. Overall, the dorsum is grayish brown, finely reticulated in some parts because some scales (especially on the flanks) are dark-edged. The venter is yellowish white with prominent narrow black lines across the posterior and anterior edges of each ventral (posterior lines overlap the anterior line of the next ventral so that there is the appearance of a single line). The ventral surface of the tail is patterned similar to that of body, with blackish suture lines. A dark grayish head cap extends down to upper edges of supralabials, most of which are yellowish white.

Etymology. The species name *paucicarinatum* is a Latin adjective of neuter gender derived from the words *paucus* (few or little) and *carinatus* (keeled or ridged).

Cope (1894: 203) referred to the "... much smaller number of more feebly keeled scales" in *Drymobius paucicarinatus* compared with the previously described species, *Drymobius percarinatus* Cope. Thus, he seems to have intended the name to refer to both the fewer number of keeled dorsal rows and the weaker keels of the new species compared with *Dendrophidion percarinatum* ("very keeled"). Although Cope (1894) compared the species explicitly only with *D. percarinatum*, keels in *D. paucicarinatum* are weaker than in any other species of the genus except perhaps some individuals of *D. bivittatum*.

Diagnosis and Comparisons. Dendrophidion paucicarinatum is characterized by (1) dorsocaudal reduction from 8 to 6 occurring anterior to subcaudal 25 (range, 2–23); (2) divided anal plate; (3) ventrals >175 in males and females; (4) subcaudal counts <140 in males and females; (5) dorsal keels very weak and restricted to few dorsal rows anteriorly and at midbody (keels usually absent on the neck); (6) pale dorsal crossbands absent; subadults often with a series of dark crossbands or middorsal blotches alternating with a lateral series of dark blotches; adults generally more uniform in dorsal coloration, greenish or brownish; adults and many juveniles with prominent, narrow, dark transverse ventral lines; (7) everted hemipenis of the "robust" morphology (Cadle, 2012b: 266 and fig. 2), with a relatively short, narrow hemipenial body proximal to a bulbous region bearing spines, calyces, and other apical ornamentation; spinose region delimited distally by a relatively uniform row of larger spines; total number of spines >80.

Dendrophidion paucicarinatum differs from eight species of the *D. dendrophis* species group (*D. dendrophis, D. atlantica, D. nuchale, D. clarkii, D. rufiterminorum, D. apharocybe, D. crybelum, D. vinitor*) in having a more proximal reduction in the dorsocaudal scales (nearly always distal to subcaudal 30 in the *D. dendrophis* species group); in having a greater number of ventrals (>175 compared with ≤175 in the *D. dendrophis* species group); and in

having much more weakly keeled dorsal scales (very strongly keeled in the *D. dendrophis* group). A divided anal plate will distinguish *D. paucicarinatum* from *D. apharocybe, D. crybelum*, and *D. vinitor* (anal plate nearly always single in these species). *Dendrophidion paucicarinatum* differs from *D. boshelli* in having 17 midbody scale rows (15 in *D. boshelli*).

Dendrophidion paucicarinatum differs from *D. percarinatum* in aspects of color pattern and segmental counts, as follows (characters of *D. percarinatum* in parentheses): dorsum in adults usually somewhat uniformly colored, and lacking distinct pale crossbands or dark dorsal lines (pale crossbands usually present anteriorly and dark lines posteriorly; see Cadle, 2012b); narrow dark lines across the posterior edge of each ventral in adults and many juveniles (venter relatively immaculate except for lateral spots or dark pigment); and ventrals >175 (nearly always <170 except occasional individuals from Panama and Colombia; Cadle, 2012b). Dorsal scales are much more strongly keeled and encompass more dorsal rows in *D. percarinatum* than in *D. paucicarinatum*.

Dendrophidion paucicarinatum differs from all other members of the *D. percarinatum* species group in having a greater number of ventrals (>175). It averages fewer subcaudals than other species of the *D. percarinatum* group except *D. bivittatum*; a low number of subcaudals (<140) will distinguish *D. paucicarinatum* from most individual specimens of the *D. percarinatum* group except some *D. bivittatum* and *D. graciliverpa. Dendrophidion bivittatum* differs from *D. paucicarinatum* in having prominent blackish dorsolateral and lateral stripes on the posterior body. *Dendrophidion graciliverpa* and *D. prolixum* differ from *D. paucicarinatum* in having a hemipenis of "gracile" morphology (Cadle, 2012b: 266 and fig. 2) and different color patterns. All species of the *D. percarinatum* group that have dark transverse ventral lines similar to those of *D. paucicarinatum* (i.e., some adults of *D. graciliverpa, D. prolixum*, and *D. brunneum*) are South American species.

Taxonomic Description (28 males, 40 females, 5 unsexed juveniles). Table 1 summarizes size, body proportions, and meristic data for *D. paucicarinatum*; sexual dimorphism in some characters is summarized in the next section. Largest specimen (Natural History Museum of Los Angeles County [LACM] 149213) a female 1,527 mm total length, 1,021 mm SVL. Largest male (LACM 149217) 1,235 mm total length, 824 mm SVL. Tail 32–37% of total length (46–58% of SVL) in males; 31–35% of total length (46–54% of SVL) in females. Tails are proportionally shorter in small individuals. Specimens less than 300 mm SVL have tail lengths 29–32% of total length, 41–46% of SVL ($N = 12$, males and females combined).

Dorsal scales nearly always in 17–17–15 scale rows, the posterior reduction usually by fusion of rows $3 + 4$ ($N = 23$) or $2 + 3$ ($N = 3$) at the level of ventrals 92–109. Ventrals 178–195 (averaging 187.0) in males, 180–189 (averaging 184.0) in females; usually one preventral anterior to ventrals (70.6% of specimens), with lower frequencies of zero (19.6%), two (7.8%), or three (2%). Anal plate divided. Subcaudals 120–139 (averaging 127.4) in males, 120–137 (averaging 128.3) in females. Dorsocaudal reduction at subcaudals 6–23 in males (mean 12.6), 2–15 in females (mean 8.0). Preoculars one, postoculars nearly always two, primary temporals usually two, secondary temporals two, supralabials usually nine with four to six bordering the eye (occasionally other patterns with 8 or 10 supralabials; Table 1), infralabials usually 10 (moderate frequency of 9 or 11, rarely 8). Supralabial/temporal pattern (Cadle, 2012b) overwhelmingly the *P*-pattern (Table 1). Maxillary teeth 33–41 (averaging 38), typically with three or four (occasionally five) posterior teeth enlarged. Enlarged teeth are ungrooved, not offset, and a diastema is absent. Lieb (1988, 1991) and Savage (2002) stated that the anal plate is "usually divided" in *D. paucicarinatum*, suggesting some variation; none of 58 specimens for which we scored this character had a single anal plate.

Fusions or divisions of temporal scales were infrequent. Counting each side of the head separately, 11.8% of the upper secondary temporals were divided vertically. Another 14.5% of the sides had other unusual divisions or arrangements, including partial sutures in the temporals, other simple fusions or divisions among the temporals, lower primary temporals contacting a parietal scale, an upper labial divided horizontally, or irregular divisions of temporals.

Two apical pits are present on dorsal scales. Of 32 specimens scored for keeling, 88% ($N = 28$) lacked keels entirely on the dorsal rows of the neck; the remainder had only the vertebral row ($N = 2$) or the vertebral + paravertebral rows ($N = 2$) keeled on the neck. At midbody 15.7% ($N = 5$) had keels on all rows except rows one or one to two; 18.8% ($N = 6$) lacked keels on the first three rows; 62.6% ($N = 20$) lacked keels on the lower four to seven dorsal rows; and one specimen lacked keels on all midbody dorsal rows. Posteriorly, half of the specimens had keels on all rows except row one; 34.4% ($N = 11$) had keels on all rows except rows one to two or one to three; 12.6% ($N = 4$) lacked keels on rows one to four or one to five; and one specimen lacked keels entirely on the posterior body. Keels are weaker on the dorsal scales of *D. paucicarinatum* than in other species of *Dendrophidion* with the possible exception of *D. bivittatum*. Some keels on lower dorsal rows extended only part of the length of the scales, and keels on lower dorsal rows were often very weak even when present. There is some suggestion that keeling is less developed in females than in males. Three of four specimens that had keels on scales of the neck were males, and females often had fewer rows keeled at midbody and posteriorly than did males. One juvenile female had no detectable keels on any dorsal rows.

Hemipenis (described in detail later herein) unilobed with a bulbous apex; overall morphology "robust" (Cadle, 2012b: 266). Spinose region followed distally by flounces and calyces. Tip of the apex largely nude. Sulcus spermaticus simple, centrolineal, and having a slightly flared tip in everted organs. Retracted hemipenis extending to the middle

TABLE 1.   TAXONOMIC DATA FOR *DENDROPHIDION PAUCICARINATUM*.
BODY PROPORTIONS, SEGMENTAL COUNTS, SCALE REDUCTIONS,
MAXILLARY TEETH, AND NUMBER OF PALE BANDS ARE GIVEN AS RANGE
FOLLOWED BY MEAN ± SD. BILATERAL COUNTS ARE SEPARATED BY A SLASH
(/). FOR TEMPORALS AND LABIAL SCALES, EACH SIDE OF A SPECIMEN WAS
COUNTED AS AN INDEPENDENT OBSERVATION. SAMPLE SIZES ARE IN
PARENTHESES. ASTERISKS INDICATE STATISTICAL SIGNIFICANCE OF
DIFFERENCES BETWEEN MEANS OF MALE AND FEMALE SIZE OR MERISTIC
COUNTS (STUDENT'S *t* TEST); OR RELATIVE TAIL LENGTHS (MANN–
WHITNEY *U* TEST). *** $p < 0.001$; n.s., no significant difference.

Parameter	*Dendrophidion paucicarinatum* (Cope)
Largest specimens: total length, snout–vent length (SVL) (mm)	
Male	1,235, 824
Female	1,527, 1,021
Mean adult SVL (mm)	
Male	535–824 645.0 ± 67.99 (18)***
Female	518–1021 753.8 ± 109.43 (32)
Tail length/total length	
Male	0.32–0.37 0.34 ± 0.018 (12) n.s.
Female	0.31–0.35 0.33 ± 0.011 (25)
Tail length /SVL	
Male	0.46–0.58 0.51 ± 0.040 (12) n.s.
Female	0.46–0.54 0.50 ± 0.024 (25)
Maxillary teeth	33–41 37.9 ± 2.15 (23)
Dorsal scales	17–17–15 (52) 17–17–13 (1)
Ventrals	
Male	178–195 187.0 ± 4.07 (28)***
Female	180–189 184.0 ± 2.64 (40)
Subcaudals	
Male	120–139 127.4 ± 5.40 (18) n.s.
Female	120–137 128.3 ± 3.82 (28)
Total segmental counts (ventrals + subcaudals)	
Male	307–330 315.3 ± 5.26 (18) n.s.

TABLE 1.   CONTINUED.

Parameter	*Dendrophidion paucicarinatum* (Cope)
Female	303–323 312.8 ± 4.94 (28)
Dorsocaudal reduction, 8 to 6 (subcaudal number)	
Male	6–23 12.6 ± 4.48 (26)***
Female	2–15 7.97 ± 2.45 (39)
Dorsal scales, posterior reduction (ventral number)	
Male	94–102 99.2 ± 3.37 (6) n.s.
Female	92–109 101.1 ± 4.32 (20)
Preoculars	1/1 (53)
Postoculars	1/2 (1) 2/2 (52)
Primary temporals	1 (3) 2 (103)
Secondary temporals	2 (106)
Supralabials, supralabials touching eye	8, 3–5 (5) 8, 4–5 (1) 9, 4–6 (99) 10, 5–7 (1)
Infralabials	8 (1) 9 (12) 10 (75) 11 (18)
Supralabial/temporal pattern (Cadle, 2012b)	G, 10.3% P, 73.5% Irregular/ambiguous, 16.2% (68)
Hemipenial characters	Robust morphotype >80 enlarged spines

of subcaudal 8 up to the distal portion of subcaudal 10.

Sexual Dimorphism. A suggested sexual difference in the degree of keeling on the dorsal scales mentioned above needs further quantification. Sexual dimorphism in the degree of keeling on dorsal scales in snakes has been reported infrequently, but does occur in some species (for a brief discussion see Layne and Steiner, 1984).

Statistically significant sexually dimorphic characters are the following (Table 1): mean adult SVL (female greater; $t = 4.33$, df =
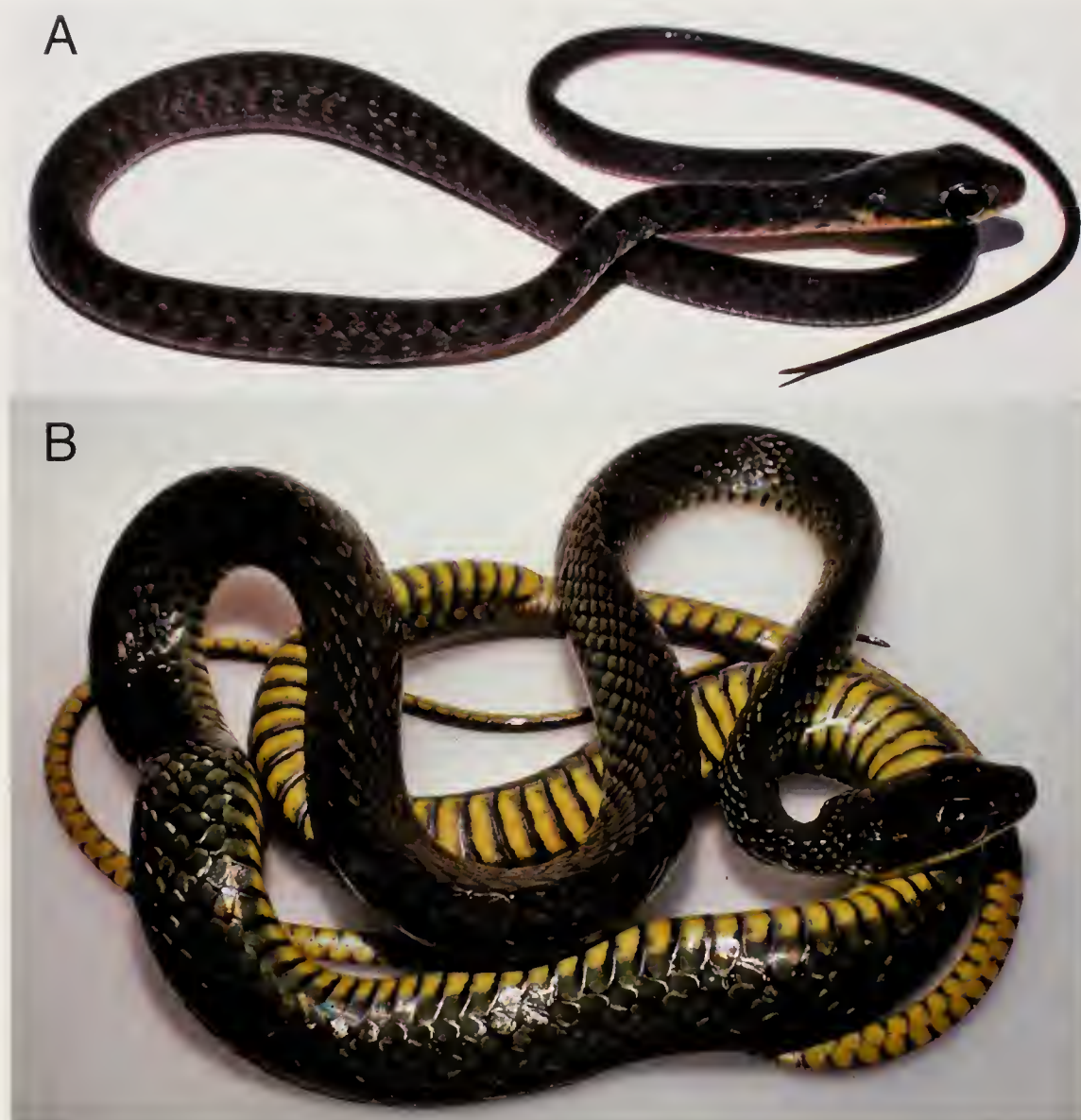
Figure 2.   *Dendrophidion paucicarinatum* in life. A, AMNH R-114315 (juvenile male from Chiriquí Province, Panama; 221 mm SVL). B, AMNH R-124011 (adult female from Chiriquí Province, Panama; 755 mm SVL). Photographs by Charles W. Myers.

48; $P < 0.0001$), ventral counts (male greater; $t = 3.44$, df $= 66$; $P = 0.001296$), and the point of dorsocaudal reduction (male more distal; $t = 4.78$, df $= 63$; $P < 0.0001$). Among 10 other species of *Dendrophidion* in which sexual dimorphism has been examined in detail (Cadle, 2010, 2012a,b; Cadle and Savage, 2012), female superiority in body size is found only in *D. brunneum* and *D. graciliverpa* (other species are not dimorphic in body size) and male superiority in ventral counts is unique to *D. paucicarinatum* (females superior in all other species). Male superiority in ventral counts and lack of sexual dimorphism in subcaudal counts or RTL are also less common patterns among colubrids generally (Shine, 1993, 1994). Other species of *Dendrophidion* are sexually dimorphic in the point at which the reduction in dorsal scale counts occurs, but failure

to detect a significant difference for *D. paucicarinatum* may be due to the small sample of males (Table 1).

Coloration in Life. A sampling of published color photographs of *D. paucicarinatum* includes Savage (2002: pl. 417), Solórzano (2004: 236, figs. 57–58), and Köhler (2003: fig. 477) from Costa Rica; and Köhler (2008: fig. 578) from Panama. Specimens from Panama are illustrated in Fig. 2.

The dorsum of adults is generally brown to green or grayish, appearing more or less uniform or with a finely reticulated or speckled appearance. The venter is washed with pale to bright yellow and each ventral bears a narrow dark transverse line across its anterior and posterior edges (Figs. 2–3). Juveniles are greenish to brown and have a series of transverse narrow (less than two scales wide) blackish blotches or bands, often

Figure 3. Dorsal patterns in adult and subadult specimens of *Dendrophidion paucicarinatum*. A, AMNH R-124013 (Panama, 741 mm SVL). B, KU 107657 (Panama, 550 mm SVL). C, UMMZ 155733 (Panama, 903 mm SVL). D, LACM 149224 (Costa Rica, 385 mm SVL).

with a middorsal series alternating with an offset lateral series (Fig. 2A). Juveniles have a yellow to gray or whitish venter and many exhibit a less distinct version of the dark transverse lines that are prominent in adults (sometimes interrupted midventrally or occasionally absent in juveniles).

The following color notes for Panamanian specimens are from the field notes of Charles W. Myers:

AMNH R-114315 (juvenile male, 221 mm SVL. Fig. 2A). Head brown, neck dull green, turning brown on rest of body—the length of which is marked with numerous black crossbands. Ventrolateral black line forming on rear of body and becoming sharper on tail. Supralabials, underside of head, and anterior venter yellow, turning grayish white posteriorly. Iris dark brown except upper fifth sector, which is pale green. Tongue dark blue with black fork.

AMNH R-114316 (juvenile female, 243 mm SVL). Brown head, green neck, and brown body with posterior lateral black

Figure 4.   Head pattern of *Dendrophidion paucicarinatum*. AMNH R-124013.

line. Labials, under head and neck bright yellow, turning greenish gray and, finally, light brown under venter and tail. Iris tan on upper 1/5, dark brown below. Tongue dark blue with black fork.

University of Kansas Museum of Natural History (KU) 107657–58 (adult males, 550 and 700 mm SVL; notes from specimens that had been dead for several hours but before preservation). Brownish above. Chin and throat bright yellow. Supralabials and rest of venter light yellow, with black transverse lines on venter. Iris tan on upper 1/4, brown below. Tongue blackish.

AMNH R-124011–12 (adult females, 755 and 751 mm SVL; Fig. 2B). Head brown; body green with brown suffusion dorsally; some white scale edges impart a slightly speckled aspect. Lips, underside of head, venter, and underside of tail greenish yellow; ventrals and subcaudals with black

transverse lines. Tongue black (including tips).

AMNH R-124013 (adult female, 741 mm SVL). Color similar to AMNH R-124011–12.

AMNH R-129756 (adult female, 750 mm SVL). Dark olive green above. Supralabials, underside of head, and ventral surfaces greenish yellow, with black transverse lines on ventrals and subcaudals. Iris pale tan on upper 1/4, dark reddish brown below. Tongue, including tips, black.

The general dorsal coloration of *D. paucicarinatum* clearly varies (green, brown, gray), as can be seen by inspection of published photographs and the above descriptions. It is less clear whether there is a geographic or ontogenetic component to this variation. Color notes quoted above seem to suggest that juveniles and smaller adults in western Panama (AMNH R-114315–16, KU 107657–58) are more generally brown dorsally, whereas the larger individuals (AMNH R-124011–13, R-129756) are greener. However, Slevin (1942) indicated no such subtlety in describing the coloration of *D. paucicarinatum* from the vicinity of Boquete (Chiriquí, Panama) as uniform brown dorsally, the undersurfaces of the body and tail yellowish, and the posterior edge of the ventrals and
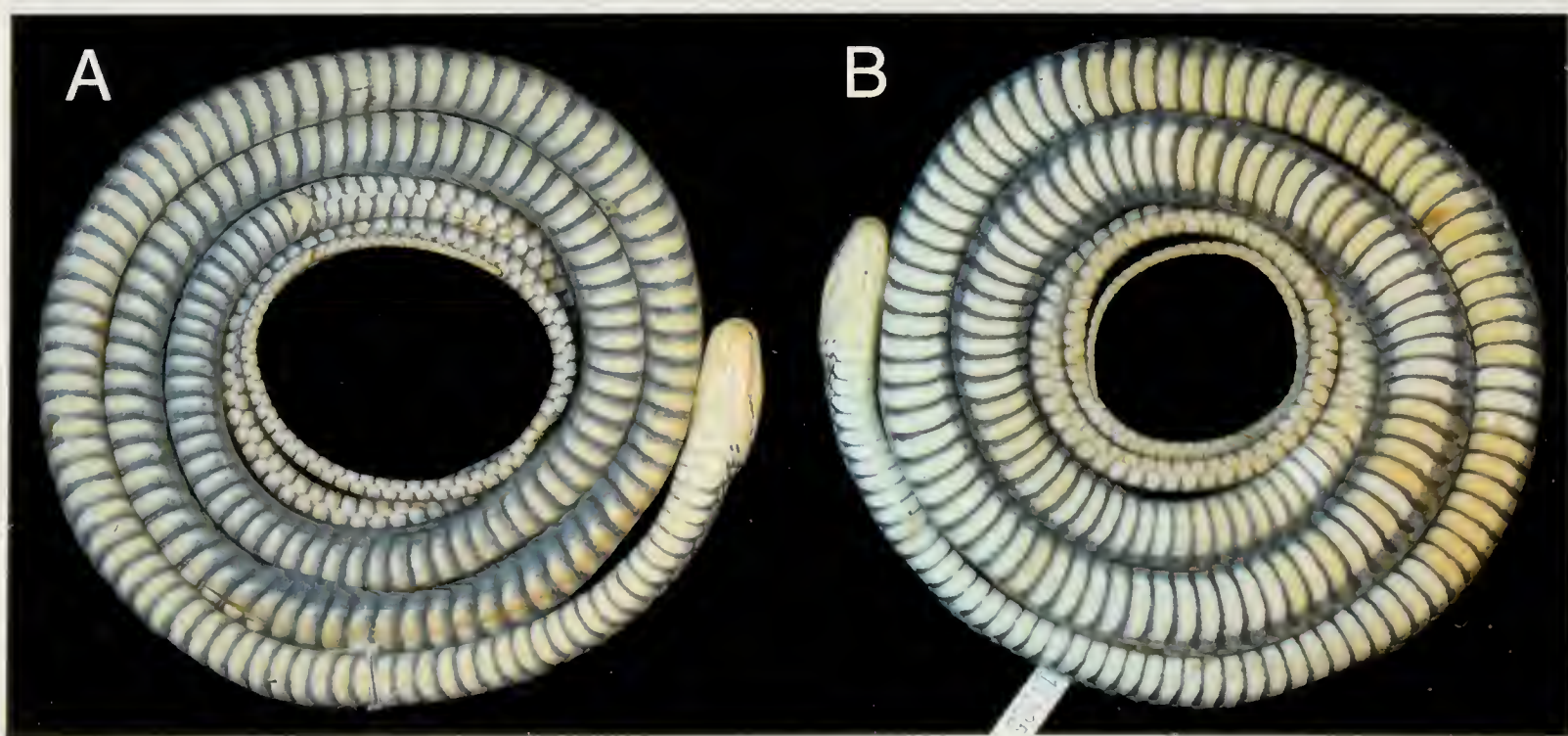

Figure 5.   Ventral patterns in adult specimens of *Dendrophidion paucicarinatum* (Panama). A, UMMZ 155733. B, AMNH R-124013. See Figure 3 for size measurements.

Figure 6.   Juvenile patterns in *Dendrophidion paucicarinatum*. A, B, dorsal views (Costa Rica); C, D, ventral views (Costa Rica and Panama, respectively). A, LACM 149228 (268 mm SVL). B, KU 63809 (260 mm SVL). C, AMNH R-114316 (243 mm SVL). D, KU 63809 (260 mm SVL). Note the difference in the prominence of the transverse lines in C and D.

subcaudals with a narrow black border (five specimens from Slevin's collection in the California Academy of Sciences [CAS] are adults 600–900 mm SVL). Hayes et al. (1989: 50) indicated that in the vicinity of the Monteverde Cloud Forest Preserve (Costa Rica) snakes nearer the continental divide tended toward greener shades, whereas the snakes were browner at lower elevations to the west; however, it is not clear whether these authors considered body size as a covariate of coloration.

Coloration in Preservative. Preserved adults are brownish with intact stratum corneum and gray to blue-gray without the stratum corneum (Fig. 3). Sometimes the dorsal scales are black-tipped and the dorsum may appear finely or more coarsely reticulated. Evidence of the juvenile dorsal pattern of dark crossbands is retained in
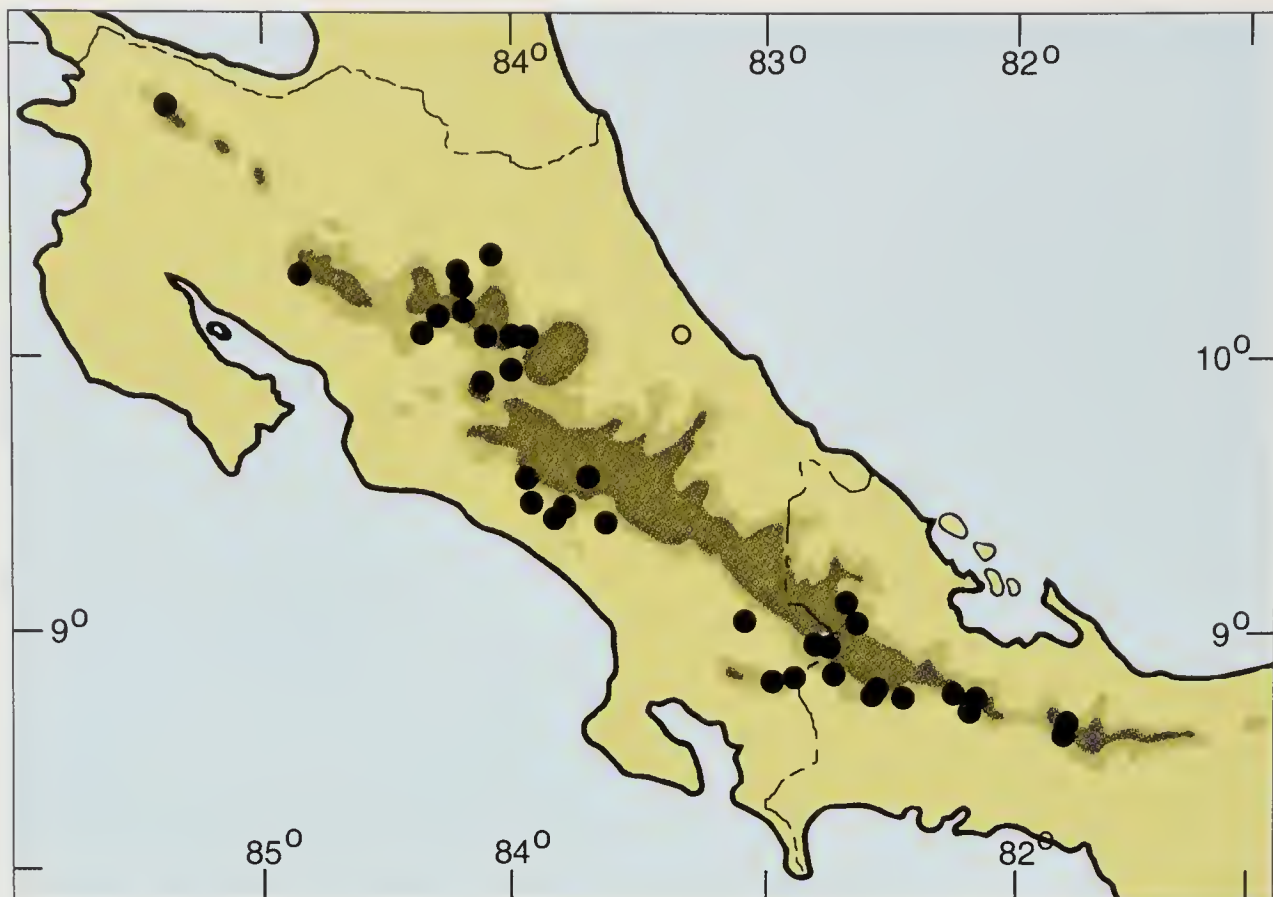
Figure 7.   Distribution of *Dendrophidion paucicarinatum* in Costa Rica and western Panama. Pale gray shading is 1,000–1,500 m; darker gray is 1,500–3,000 m. Open circle in eastern Costa Rica just north of 10° latitude is Sara, a questioned locality for *D. paucicarinatum* (see Distribution).

some adults (e.g., Figs. 3B, 8) but not all (Figs. 3A, C). There is usually a blackish postocular bar extending diagonally to the last supralabial (Fig 4). The venter has dense black transverse lines. Each line comprises a heavy black line on the posterior edge of each ventral, which overlaps a lighter line on the anterior edge of next distal ventral (Fig. 5).

Juveniles (Fig. 6) have narrow dorsal and lateral blotches or wavy bands, which often form a reticulate network. The venter is whitish with or without narrow dark transverse lines. The lines are less dense, especially midventrally, in juveniles compared with adults.

Distribution. The geographic range of *D. paucicarinatum* (Fig. 7) in Costa Rica includes the Atlantic and Pacific slopes of the Cordillera Central and Cordillera de Tilarán; extreme northwestern extent of the Cordillera Guanacaste (Cerro Cacao); and the Pacific slope of the Cordillera Talamanca, whence the distribution continues into western Panama (Chiriquí Province) along the Pacific slopes of this massif. Other known Panamanian localities include the

Pacific slopes and continental divide in the Cerro Fortuna area (extreme eastern end of the Cordillera Talamanca) and Cerro Colorado area (Serranía de Tabasará), the easternmost known locale. The only definitive Atlantic-slope localities in Panama are on the northeastern slope of Cerro Pando in Bocas del Toro Province, Panama. Nearly all records of *D. paucicarinatum* are above 1,000-m elevation, with the upper elevational record represented by UCR 6256 from 2,360 m (San José Province, Costa Rica). The lowest unambiguous record is LACM 149215 from 850-m elevation (Heredia Province, Costa Rica).

One Costa Rican specimen, Museum of Vertebrate Zoology (MVZ) 36450 (incorrectly cited as AMNH 36450 by Savage [2002: 657]), is reputedly from a lowland locality so far outside the rest of the known geographic and elevational range of *D. paucicarinatum* that we are inclined to believe the locality data are in error. The specimen (Fig. 8), collected by the botanist H. E. Stork during August 1932, supposedly is from "Sara (Madre de Dios)," Limón

Figure 8. *Dendrophidion paucicarinatum*, MVZ 36450 (adult male, 611 mm SVL), reportedly from "Sara (Madre de Dios)," a lowland locality in Limón Province, eastern Costa Rica (here considered erroneous).

Province, in the Atlantic lowlands at about 40-m elevation (Fig. 7, open circle). However, the specimen was received and catalogued into the MVZ collection only in 1941, and locality data were secured via correspondence between E. Raymond Hall and Stork only at that time (accession records and correspondence, MVZ archives, kindly provided by Carol Spencer and David Wake). Upon receipt, MVZ 36450 was in a jar containing several other lizards and snakes. We suspect some error crept into the data about the specimen's origin at that point, but this is an inference based solely on the unusual distributional record suggested by the specimen itself. In any case, no other record of *D. paucicarinatum* is from below 840-m elevation. Savage (2002: 657) commented on several other erroneous records in the literature of this species based on misidentified specimens.

There are no substantiated records of *D. paucicarinatum* from the Atlantic slopes of the Cordillera de Talamanca in Costa Rica, and few records from the low volcanic peaks of northwestern Costa Rica. The absence of records from the Atlantic slope of the Cordillera de Talamanca of Costa Rica is puzzling. The dense premontane and lower montane forests of these uplands are similar to, and contiguous with, those of the Atlantic versant in western Panama, where *D. paucicarinatum* occurs on the north slopes of Cerro

Pando near the Costa Rica–Panama border (Appendix 1 and Fig. 7). However, few collections have been made from the Atlantic versant of the Talamanca range in Costa Rica, a wild region that can, for the most part, only be accessed on foot trails. The rugged and steep terrain and an annual rainfall of over 4 m make fieldwork in this area extremely difficult and we think the absence of records reflects inadequate sampling.

Known localities for *D. paucicarinatum* are all from premontane and lower montane evergreen forest sites. The presence of this species on Volcán Cacao in northwestern Costa Rica suggests that it will be found on the slopes and peaks of other mountains in the Cordillera de Guanacaste (Cerros Orosí and Rincón de la Vieja and Volcanes Miravalles, Tenorio, and perhaps the currently active Volcán Arenal). *Dendrophidion paucicarinatum* is likely to be found at lower elevations at these sites than elsewhere because of a temperature depression caused by the flow of the northeast trade winds through the gaps between the solitary peaks. The currently known range limit of *D. paucicarinatum* in western Panama is Cerro Colorado, Comarca Ngäbe-Buglé (approximately 81°48'W). However, suitable habitat for *D. paucicarinatum* is found at least as far as the eastern end of the Serranía Tabasará near El Copé, Coclé Province (approximately 80°36'W), but

fieldwork by Karen Lips, Roberto Ibáñez, and their associates have failed to find this species east of the Cerro Colorado/Cerro Santiago area.

NATURAL HISTORY OF *DENDROPHIDION PAUCICARINATUM*

Little has been reported concerning the natural history of *D. paucicarinatum* (Savage, 2002: 656–657; Solórzano, 2004: 232–234). Goldberg (2003) summarized some reproductive parameters. Like other species of *Dendrophidion*, *D. paucicarinatum* is diurnal, terrestrial (sometimes said to climb into low vegetation), and a predator upon frogs. AMNH R-73329 contained the hind limbs of a large frog in its stomach, referred to *Craugastor rugosus* (Craugastoridae) on the basis of distinctive dark ventral spots and blotching; AMNH R-129756 had a large frog (not identified) in its stomach.

Brief field notes recorded for Panamanian specimens by Charles W. Myers are the following: active during the day on a new road through cloud forest (AMNH R-124011–12; 1,050–1,100 m); dead on a road on the relatively dry western side of Cerro Hornito with patches of forest (not cloud forest) nearby (AMNH R-129754; 1,100 m); on the ground by day in cloud forest (AMNH R-129755; 1,250–1,400 m); active about 2:00 p.m. on the ground in light rain in cloud forest (AMNH R-129756; 1,250–1,410 m).

The frequency of broken/healed tails in our sample of *D. paucicarinatum* is 18.5% (10 of 54 specimens). This frequency is comparable with other species of *Dendrophidion* with relatively short tails, e.g., the six species in the *D. vinitor* and *D. nuchale* complexes (Cadle, 2012a; Cadle and Savage, 2012), in which frequencies of broken tails are 6.7–16%. Tail breakage frequencies in relatively long-tailed species such as *D. brunneum*, *D. percarinatum*, or *D. dendrophis* are much higher (>35%; Cadle, 2010 and unpublished data; Stafford, 2003; Prudente et al., 2007).

Habitats of *D. paucicarinatum* are usually characterized as premontane or lower montane wet forest in the Holdridge system (Holdridge, 1967), montane rain forest, or cloud forest. The known localities receive considerable precipitation in the form of rainfall with, at some localities, additional precipitation from cloud moisture. Rainfall estimates for sites from which *D. paucicarinatum* is known (Las Cruces region of southwestern Costa Rica and the Cerro Fortuna region of western Panama) are 4,000 mm or more (Scott, 1976; Myers and Duellman, 1982: 12); rainfall in the vicinity of Monteverde, Costa Rica averages somewhat less (3,000+ mm) but that estimate does not include substantial precipitation from cloud moisture (Clark et al., 2000). A summary of other habitat characteristics of the Las Cruces region is given in Cadle (2012a: 216–217) and details for the Monteverde region in Clark et al. (2000).

Charles W. Myers obtained eight specimens from the Cerro Fortuna area of western Panama (Cerro Fortuna, Quebrada de Arena, Cerro Hornito) along a transect 1,000–1,500 m in elevation. Myers and Duellman (1982: 12 ff.) described the area in detail:

... work was conducted principally on the northeastern base of Cerro Fortuna, at a proposed dam site on the upper Río Chiriquí (about 23 km NNE Gualaca, Chiriquí), at about 1000 m. above sea level. ... Preliminary data for the dam site indicate a high average rainfall in excess of 4000 mm., with an average temperature of about 16°C. in a range of about 11–23°C. ... Apparently there is no real dry season. Rain fell daily at the dam site in February 1976, at a time when the adjacent Pacific lowlands were ... in the midst of the annual dry season. Occasional days were clear and sunny, with precipitation falling only in a *bajareque* in late afternoon, but usually there were also spells of cold, drenching rain. This climate is classifiable as Temperate Wet (*Cf*) under the Köppen system ... [and] the forest of this high, Pacific-drainage watershed is physiognomically classifiable as Lower Montane Rain Forest .... The forest is comprised of

tall, straight-boled trees, with a high canopy approaching 30 m. on favorable slopes. Buttressed roots are common but of smaller average size than is characteristic of Lowland Rain Forest; large stilt roots and spiny trunks are decidedly uncommon. Vascular epiphytes are abundant, even growing low on the tree trunks in some areas, but the tree trunk "moss" layer is relatively sparse. On gentle slopes, the forest tends to be fairly open, with few saplings and treelets but with a dense ground cover of ferns and herbaceous vegetation growing to a height of about 1 m.; but in many places, particularly on steep slopes, there is a much denser woody undergrowth... Tree ferns and palms are scattered, with some palms penetrating the high canopy. However, compared with the situation usually encountered (in Panama) in both higher and lower-elevation wet forest, palms are relatively scarce, growing densely only in apparently rare groves of "*guagara*" palm. This forest is replaced on the summit of Cerro Fortuna (1400–1500 m.) by a denser, more luxuriant cloud forest, which has a lower canopy and a rather stunted and twisted aspect, physiognomically approaching Montane Thicket.

For the same area Myers et al. (1984: 13 and fig. 8) add:

"The habitat on the continental divide is a much cooler cloud forest (fig. 8), which receives almost daily fog that is frequently accompanied by rain and mist. This cloud forest is a facies of high-canopied lower montane rain forest. Tree growth is very dense, and there is a frequently dense herbaceous and fern layer at ground level. There is a modest "moss layer" on the trunks of trees, which support a profusion of epiphytic growth, including bromeliads. There are few bromeliads near the ground, although they are common higher in the trees, especially above 10 m."

Myers (1969: 33–35 and fig. 17) and Trueb (1968: 285) described the forest at another collecting locale of *D. paucicarinatum* at 1,450 m on the Atlantic slope of Cerro Pando (western Panama near the international border with Costa Rica). Myers referred to the

forest as "lower montane rain forest" and stated that "below 1800 meters ... the moss on trunks thins out ... and palms become relatively scarce. Although Trueb (1968: 285) mentioned 'an understory of palms' in the forest at 1450 meters elevation, it is difficult to find sufficient palms for the thatching of any but the smallest of shelters. Heavy rains occurred at our lower camps, in contrast to the usual mist or light rains of the upper region." Trueb (1968: 285) added that "the forest consists of some large trees (heights of 35 m) and ... in comparison with the forest at 1920 m, the herbaceous ground-cover is better developed, and moss is less conspicuous. ... Some palms and small trees occur along the edges of the streams, but herbs and dense tangles of bushes are most conspicuous there."

Goldberg (2003) reported clutch sizes of 3 to 12 for four specimens from Costa Rica. Gravid females with enlarged ($\geq$15mm) or oviductal eggs that we examined (11 specimens) were collected between 18 April and 13 August. Clutch sizes and associated SVLs for those for which we determined clutch sizes are: 3 (759 mm, LACM 149219), 6 (741 mm, AMNH R-124013), about 6 (841 mm, AMNH R-17268), 9 (922 mm, LACM 149222), 12 (1,021 mm, LACM 149213), and 12 (950 mm, LACM 149215). Two females (SVLs of 625 mm and 906 mm) had no eggs but had convoluted oviducts, which indicates that they were sexually mature. CAS 78899, the larger of these two, was collected 25 July 1939 and had expanded oviducts, suggesting that it had recently laid a clutch of eggs. Goldberg (2003) inferred that multiple clutches per year might be produced on the basis of LACM 149219, which had vitellogenic ovarian follicles in addition to oviductal eggs. Males undergoing spermiogenesis were collected in July and early October (Goldberg, 2003), and had SVLs of 648–824 mm. A male that we examined with SVL of 643 mm (AMNH R-73327) collected in January 1953 had convoluted vasa deferentia, which indicates sexual maturity in males. Thus, the smallest male and female of *D. paucicarinatum* that had indications of sexual maturity were 643 mm and 625 mm SVL, respectively.

Four specimens <250 mm SVL (323–355 mm total length) for which the date of collection is known were collected January–March, whereas three specimens 250–299 mm SVL (391–424+ mm total length) were collected June–August. The smallest specimen we examined was 201 mm SVL (no collection date available). We suspect that those collected January–March may have recently hatched, as Solórzano (2004: 233) illustrated a neonate with a total length of 361.

HISTORICAL AND PRESENT POPULATION TRENDS

Most of the known specimens of *D. paucicarinatum* from Panama have come from the vicinity of the town of Boquete, Chiriquí Province, and the nearby "Lérida Farm" (Slevin, 1942; Dunn, 1947); more recently, Charles W. Myers obtained several specimens from mountains in this area. Slevin (1942: 472) characterized *D. paucicarinatum* from the vicinity of Boquete as "a rare species apparently confined to the forested country containing clearings for coffee growing ... found in heavy undergrowth along trails in the mountainous districts above the floor of the Caldera Valley." Slevin (1942: plate 39, fig. 1) illustrated the habitat.

On the other hand, in a sample of 540 snakes from Lérida Farm collected over a period of about 8 years as part of the Panamanian Snake Census (Dunn, 1947; Myers, 2003: 4–5), *D. paucicarinatum* comprised 14% of the Lérida sample numerically (76 specimens) (Dunn, 1947). It was the second most common snake in the sample after *Geophis brachycephalus* (255 specimens). Of course, it is impossible to extrapolate from these sorts of samples to any quantitative measure of relative abundance of species but the numerical abundance suggests that *D. paucicarinatum* was at one time common in that area (in contrast to Slevin's statement about its comparative rarity nearby in the vicinity of Boquete). Unfortunately, relatively few of the thousands of snakes collected as part of the

Census made their way into museum repositories (Myers, 2003: 4–5).

Few long-term data are available to indicate population trends in most tropical forest snakes. However, in regions that have been severely affected by declines in amphibian populations (especially frogs) there is concern about the status of frog predators, as are many snakes (Pounds, 2000; Cadle, 2012a: 217, 2012b: 334–335). *Dendrophidion paucicarinatum* was one of nine relatively common snakes at the Monteverde Cloud Forest Preserve (Costa Rica) before regional amphibian declines beginning in the late 1980s (Pounds et al., 1997; Pounds, 2000). Subsequently, all populations of diurnal frog-eating snakes for which there were quantitative data, including *D. paucicarinatum*, crashed precipitously through at least the early to mid-1990s (Pounds, 2000: 158–159).

No quantitative population data are available from any other site where *D. paucicarinatum* occurs. At the Las Cruces Biological Station this species seems never to have been common; only three specimens obtained in July 1974 are part of the Costa Rican Expeditions collections (now in LACM) assembled by Savage and colleagues. Two specimens were subsequently obtained in 1990 and 1993 at the nearby Fincas Las Tablas and Las Alturas, but a resurvey of the Las Cruces region in 2002–2004 (Santos-Barrera et al., 2008) recorded only two specimens of *D. percarinatum*, and none of three other species of *Dendrophidion* recorded historically from the region (*D. crybelum, D. clarkii,* and *D. paucicarinatum*).

HEMIPENIAL MORPHOLOGY OF *DENDROPHIDION PAUCICARINATUM*

Field-everted (LACM 149217, right hemipenis; Costa Rica), Figs. 9–10. Total length about 21 mm (base not totally stretched). Length of spinose region + apex, about 10–11 mm. "Robust" morphology (Cadle, 2012b: 266).

The hemipenis is unilobed, with an undivided centrolineal sulcus spermaticus, a
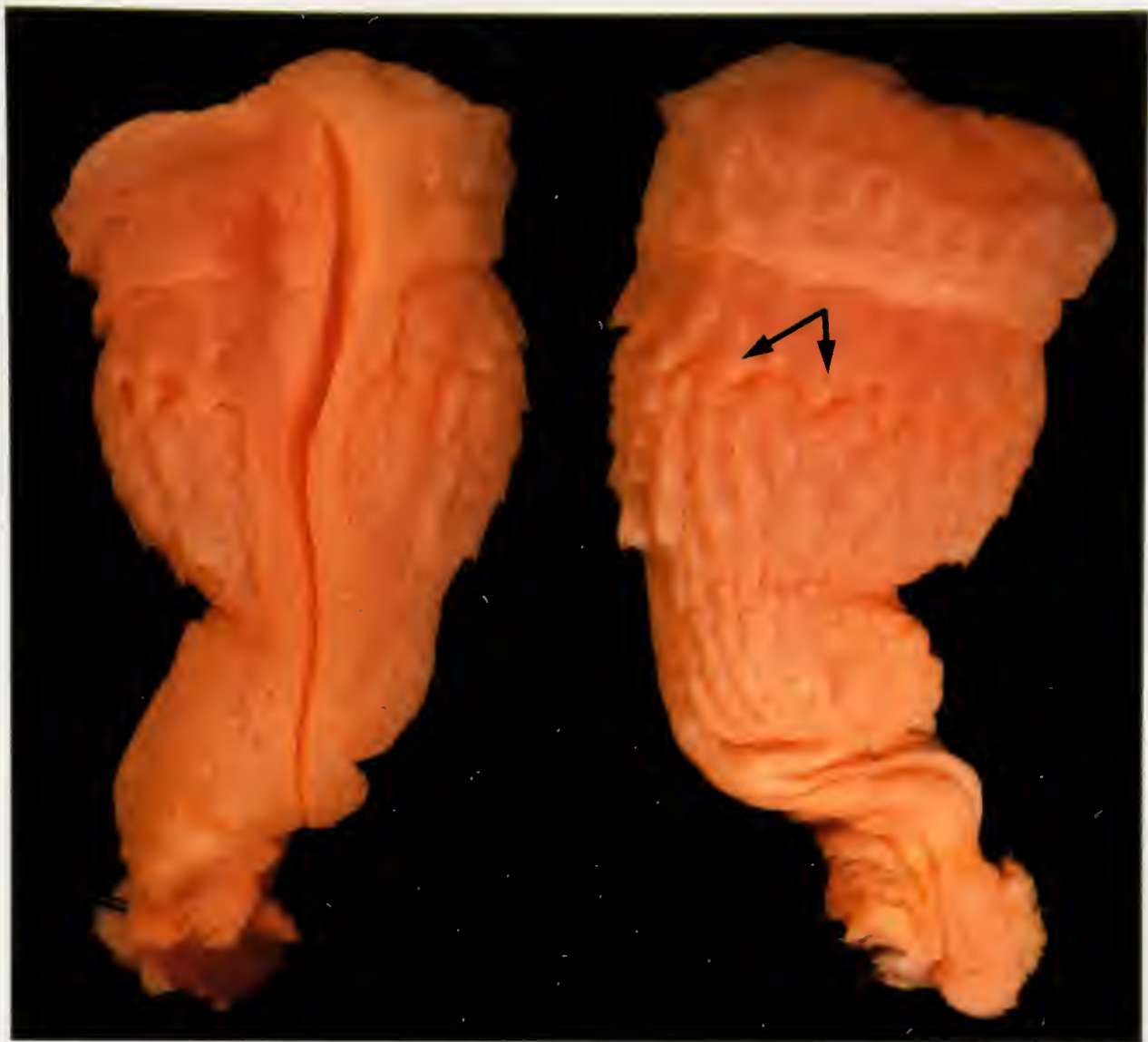
Figure 9. Everted hemipenis of *Dendrophidion paucicarinatum* in sulcate and asulcate views (LACM 149217, right hemipenis; Puntarenas Province, Costa Rica). Arrows in asulcate view indicate the spinose annulus.

narrow basal portion (slightly more than half the length of the organ), and an expanded distal region. Basal half of the hemipenial body proximal to the spines is nude; the distal half is ornamented with minute spines, which continue onto the proximal part of expanded region. These minute spines extend more proximally on the sulcate side than on the asulcate side. The "enlarged" spines in the region just proximal to the calyculate region are quite small compared with some other *Dendrophidion* hemipenes. No enlarged sulcate spines or enlarged asulcate spines are present, as in some other species (Cadle and Savage, 2012: 36).

The base of the organ has some longitudinal folds and there may be a very weakly developed nude pocket between two of the folds on the left lateral side. The folds on either side of the pocket converge toward the

base of the organ but are divergent distally; the fold on the asulcate side is slightly higher than the sulcate fold but nothing suggests a definitive lobe. The minute spines around the base of the hemipenis approach the pocket but retract around the distal end of the pocket when they reach the edge. This pocket is not as distinct as pockets on many colubrid hemipenes, and it may be an artifact produced during preservation.

The expanded distal region bears three or four rows of somewhat enlarged spines, followed by a more or less regular row of larger spines resembling a similar row seen in the *D. nuchale* and *D. dendrophis* species complexes (Cadle and Savage, 2012: 36–37). It seems appropriate to use the term spinose annulus for the distal row in *D. paucicarinatum*, as in the *D. nuchale* and *D. dendrophis* complexes (Cadle and Savage,

2012), because they are morphologically differentiated in a similar fashion and form a distinct circumferential ring in these snakes; whether the annulus in *D. paucicarinatum* is homologous to that in the other two complexes is considered later. The large spines in the annulus are interspersed with a few smaller spines, forming a less regular and sparser row of spines closely associated with, but distal to, the annulus. These distal spines mostly alternate with the spines in the annulus and are larger adjacent to the sulcus spermaticus than on the asulcate side. The total number of spines in LACM 149217 is about 106, comprising 77 enlarged spines proximal to the annulus + 29 in the annulus and its partially doubled row.

The spines are followed after a moderate gap by three thick fleshy flounces (the middle one more irregular than the proximal and distal ones). The middle flounce approaches the sulcus closely on its right side but dwindles away shortly before reaching the sulcus on the left side. On the right side of the sulcus are smooth-walled calyces between the distal pair of flounces; on the left side of the sulcus, calyces are absent adjacent to the sulcus but start soon after and continue around the asulcate side, where they become continuous with the calyces on the right sulcate side. On the asulcate side, calyces are present between the proximal pair of flounces in addition to between the distal pair.

The longitudinal walls of the calyces are thick and fleshy like those of the flounces. Longitudinal connections are more fully developed between the distal pair of flounces than between the proximal pair, the distinction in part enhanced by wider spacing between the distal pair of flounces (Fig. 9, asulcate view). No spinules (including embedded ones; see Cadle, 2010: 19; Cadle, 2012a: 218) or papillae are evident on the calyces or flounces of LACM 149217 but some variation is apparent in this feature (see below).

Distal to the flounces the apex is nude but the tissue is somewhat rugose with irregular folds, perhaps from lack of full inflation.

Figure 10. Apical view of the hemipenis of *Dendrophidion paucicarinatum* (LACM 149217). **Tss** indicates the tip of the sulcus spermaticus. Arrow indicates the scalloped edge of the apical portion of the distal flounce after it curves onto the apical tip. The apical tissue on the left side of the sulcus could not be inflated to the same extent as that on the right side (see text).

These apical folds converge on two depressions, probably the points of internal attachment of the hemipenial retractor muscles. The apical quadrant on the right side of the sulcus is more swollen than the rest of the apex because of the thicker fleshy tissue on the right side of the apex.

The sulcus spermaticus is centrolineal, with especially thick fleshy borders distally. The sulcus continues over the lip of the apex and ends on the tip of the organ between the two apical depressions (closer to the depression on the left side). On the right side of the sulcus, the distal flounce curves onto the tip of the organ as it approaches the sulcus; it is produced into a thick "shelf" with scalloped edges that partially covers the sulcus as it bends onto the apical surface (Fig. 10, arrow). The distal flounce on the left side is exaggerated similarly but not to the extent as on the right side. These extensions of the distal flounce continue to the distal end of the sulcus, gradually decreasing in prominence and thus leaving the distal tip of the sulcus exposed on the apex (unlike the portion near the edge of the apex, which is completely covered from

the right side by the thickened shelf). The tip of the sulcus is slightly expanded into a rounded terminus, but not divided; it seemingly deviates leftward on the tip of the apex and its tip is much closer to the depression on the left side than to the one on the right. The apparent asymmetry of the tissue alongside the apical portion of the sulcus is seemingly an artifact due to differential inflation of the tissue on the right side (greater) compared with the left side (not inflated at all). However, attempts to inflate the left side with warmed petroleum jelly were unsuccessful.

Variation. We examined eight other partially to fully field-everted hemipenes of *D. paucicarinatum* from Costa Rica and Panama. All are basically similar to the one just described. There is variation in the number of spines in the spinose annulus (about 15–29), with some organs having that row more or less doubled with somewhat smaller spines numbering less than 10, or smaller spines interealated within or just distal to the row. The intercalated spines in the annulus make spine counts more variable in this row for *D. paucicarinatum* than for *D. dendrophis* or *D. nuchale*, which lack intercalated spines. The total number of enlarged hemipenial spines (including the annulus) is approximately 85–110.

There are usually two to three flounces on the sulcate side of the organ, increasing to three or four on the lateral or asulcate sides; proximal flounces are broader than more distal ones. Flounces in all specimens of *D. paucicarinatum* examined are fleshy, lacking an outer membranous portion that is present in flounces of some other species of *Dendrophidion* (e.g., *D. vinitor*; Cadle, 2012a: 220). Embedded spinules are visible within some preparations, but not consistently.

Retracted (CAS 78897, Panama; right hemipenis slit midventrally and examined in situ), Fig. 11. Total length of retracted organ about 24 mm. Extends to the middle of subcaudal 10. Retractor penis magnus seemingly undivided.

Minute spines proximally, followed by a region of enlarged spines; the distal row of

Figure 11.   Retracted hemipenis of *Dendrophidion paucicarinatum* (CAS 78897, right hemipenis; Chiriquí Province, Panama).

enlarged spines (spinose annulus) has about 15 spines and these are by far the largest on the organ. Somewhat smaller spines are intercalated between larger spines in the annulus, as in the above-described everted organ. Spines are followed distally by a pair of flounces (proximal flounce much more prominent than distal flounce), and a nude apex. A partial third flounce seems to be present toward the asulcate side. Flounces are fleshy and embedded spinules were not detected in any of them. Some calyces are developed by longitudinal connections between the flounces, but these have generally poorly developed walls.

The sulcus spermaticus is simple, in the dorsolateral wall of the organ, and ends short of tip of the apex. The tip of the sulcus is slightly expanded but ends in a "box canyon"-type tip (with a distal wall of tissue

elosing off the groove of the suleus). At the level of the flounees the medial side of the suleus beeomes bordered by a broad flap of tissue (corresponding to the flap that eovers this part of the sulcus in the everted organ). A less prominent flap is present on the lateral side.

DISCUSSION

Lieb (1988) recognized two species groups within *Dendrophidion* on the basis of several scutellation and hemipenial charaeters (see above diagnosis of *D. paucicarinatum*). With the addition of newly described speeies, these groups comprise the following species:

Dendrophidion dendrophis species group: *D. dendrophis, D. atlantica* (Freire et al., 2010), three species in the *D. nuchale* complex (*D. nuchale, D. clarkii, D. rufiterminorum*; Cadle and Savage, 2012), and three species in the *D. vinitor* complex (*D. vinitor, D. apharocybe, D. crybelum*; Cadle, 2012a).

Dendrophidion percarinatum species group: *D. percarinatum, D. bivittatum, D. brunneum, D. graciliverpa* (Cadle, 2012b), *D. prolixum* (Cadle, 2012b), and *D. paucicarinatum*. Lieb (1988) left the Colombian species, *D. boshelli*, unassigned to species group.

In having weak keels on the dorsal scales and a dorsocaudal reduction proximal to subeaudal 25 in both sexes *D. paucicarinatum* resembles other species of the *D. percarinatum* group as characterized by Lieb (1988). Lieb (1988) also used a eharacter of the hemipenial spines to differentiate the *D. percarinatum* and *D. dendrophis* species groups, namely whethcr "basal hooks" were present (*D. dendrophis* group) or absent (*D. percarinatum* group). As discussed by Cadle (2012a: 228) and Cadle and Savage (2012: 36), the enormously enlarged spines on somc *Dendrophidion* hemipenes are not positioned basally as in some other snakes, but rather closer to the middle of the organ; in retracted hcmipenes the enormous spines may projcct virtually to the base of the organ, as seen in *D. clarkii* (Cadle and Savage, 2012: fig. 6). Moreover, among species of the *D. dendrophis* species group these enlarged spines are present only in *D. dendrophis, D. atlantica*, and the three species of the *D. nuchale* complex (Cadle and Savage, 2012). They are lacking in the three species of the *D. vinitor* complex (Cadle, 2012a). Thus, they do not charaeterize the *D. dendrophis* species group as a whole and instead are perhaps a synapomorphy of the *D. dendrophis + D. nuchale* species eomplexes (Cadle and Savage, 2012). Likewise, several putative hemipenial synapomorphies unite the three species of the *D. vinitor* complex (Cadle, 2012a).

In addition to enormously enlarged spines on their hemipenes, Cadle and Savage (2012) identified one othcr putative synapomorphy that characterizes hemipenes of *D. dendrophis, D. atlantica*, and all three species of the *D. nuchale* complex: the presence of a row of uniformly enlarged hcmipenial spines that delimits the distal edge of the spinose region. They termed this feature a spinose annulus because it forms a circumferential ring in everted hemipenes and a regular linear row in retracted organs that have been opened and spread flat (Cadle and Savage, 2012: figs. 6, 24–26, 28–29). Cadle and Savage (2012: 37) also pointed out that a similar row of spines was prescnt in *D. paucicarinatum*, whieh we illustrate here for the first time (Fig. 9). The spines in the spinose annulus of *D. paucicarinatum* are smaller than those in species of the *D. dendrophis* species group with the exception of *D. rufiterminorum* (Cadle and Savage, 2012: figs. 24 and 29). In addition to smaller annular spines, *D. paucicarinatum* and *D. rufiterminorum* also have a much greatcr number of spines in the annulus (22–24 in *D. rufiterminorum*, 15–29 in *D. paucicarinatum*) than do *D. dendrophis, D. atlantica, D. clarkii*, and *D. nuchale* (9–15 spincs; Cadle and Savage, 2012: 43 and Cadle, unpublished data). The annulus of *D. paucicarinatum* differs from that in the *D. dendrophis* group in having small

associated accessory spines or a partially doubled row, which accounts for some ambiguity in counts of spines in this species.

The presence of a spinose annulus in *D. paucicarinatum* and several species of the *D. dendrophis* species group could be interpreted as supporting a relationship between *D. paucicarinatum* and these other species. However, an open question is whether the annuli in all of these species are homologous. The small accessory spines intercalated among the enlarged annular spines of *D. paucicarinatum* seem to have no counterpart in the annuli of the *D. dendrophis* and *D. nuchale* complexes, which might suggest an independent origin for the annulus in *D. paucicarinatum* relative to that in the *D. dendrophis* group. In any case, the interpretation of this character will ultimately need to be reconciled with the distribution of other characters among species of *Dendrophidion* to evaluate whether the current species groups (Lieb, 1988) reflect phylogenetic entities within the genus.

Dendrophidion paucicarinatum conforms to Lieb's (1988) definition of the *D. percarinatum* group in two other characters, proximal reduction in the dorsocaudal scales and weak keels on the dorsal scales. However, there is as yet little basis for inferring whether these characters are derived for *Dendrophidion* and their support for a clade within the genus is presently ambiguous. In addition to these external characters, recent systematic revisions (Cadle, 2010, 2012a,b) suggest another putative hemipenial synapomorphy for the *D. percarinatum* species group (setting apart for the moment *D. paucicarinatum*): a common pattern of reduction in the calycular structures. Most species of the *percarinatum* group have two prominent circumferential flounces, with weak calyces sometimes present between the two flounces or distal to them, especially on the asulcate side; occasionally a partial third flounce is present toward the asulcate side. In several species (*D. brunneum, D. graciliverpa, D. prolixum*) longitudinal connections are present between calycular

structures in retracted organs but these largely disappear upon complete eversion and inflation (Cadle, 2010, 2012a,b); thus, they are pseudocalyces *sensu* Myers and Cadle (1994: 13; 2003). Reduction of calyces on the apex of species in the *D. percarinatum* group results in a largely nude apex with a few calyces left in a roughly triangular patch on its asulcate side; these are often so reduced (e.g., *D. brunneum*; Cadle, 2010) that careful inspection under a microscope is required to see them.

In contrast to the pattern just described for the *D. percarinatum* group, species of the *D. dendrophis* species group have more flounces (usually at least four) and calyces, and these are more well developed than in the *D. percarinatum* group. Up to eight flounces are present in the *D. vinitor* complex (Cadle, 2012a) and two species of this complex (*D. vinitor* and *D. crybelum*) have highly ornate apices bearing spinose ridges and other structures but no definitive calyces. Apical calyces are more reduced in *D. apharocybe* and in the three species of the *D. nuchale* complex (Cadle, 2012a; Cadle and Savage, 2012), all of which have nude expanses on the apex. More typical and well-defined calyces, many ornamented with papillae, are present to the tip of the apex in *D. dendrophis sensu lato* (Cadle, unpublished data) and *D. atlantica* (Freire et al., 2010: 65–66 and fig. 3). The presence of many well-defined papillate calyces in these last two species is unique among hemipenes of *Dendrophidion* species we have examined (Cadle, 2010, 2012a,b; Cadle and Savage, 2012, and this paper). Calyces in other species generally lack papillae, although they have embedded spinules (mineralized rods) within the calycular walls (e.g., Cadle 2010: 19 and fig. 6; 2012a: 217–220). Moreover, all *Dendrophidion* hemipenes except in the *D. dendrophis* species complex (including *D. atlantica*) and two species of the *D. vinitor* species complex (*D. vinitor* and *D. crybelum*) have large nude expanses on the tip of the apex. The apical ornamentation of *D. vinitor* and *D. crybelum* consists of arrays of oblique, freestanding

ridges unlike the regular calyces in *D. atlantica* and *D. dendrophis sensu lato*.

Dendrophidion paucicarinatum stands apart from other species of the *D. percarinatum* species group in having more fully developed calycular structures. In addition to two well-developed flounces (Fig. 9), *D. paucicarinatum* has one or two additional moderately developed (though partial) flounces and more definitive calyces than other members of the *D. percarinatum* species group; calyces are especially evident on the asulcate side (Fig. 9). In this respect the hemipenis of *D. paucicarinatum* resembles some species in the *D. dendrophis* group, although the similarity is presumably plesiomorphic for the genus (i.e., reduction in calyces is the putative apomorphic condition). Like most other *Dendrophidion* hemipenes, the apex in *D. paucicarinatum* is largely nude (Fig. 10). Thus, although several hemipenial characters of *D. paucicarinatum* resemble characters of the *D. dendrophis* species group more than they do hemipenes of other species in the *D. percarinatum* group, phylogenetic interpretation of these and the two scutellation characters defining the species groups of *Dendrophidion* (Lieb, 1988) must await broader comparisons with other Neotropical snakes. Until broader comparative work is completed, the species groups are convenient entities for purposes of discussion but their phylogenetic relevance should ultimately be tested.

ACKNOWLEDGMENTS

APPENDIX 1. SPECIMENS EXAMINED AND OTHER RECORDS OF *DENDRIOPHIDION PAUCICARINATUM*

Museum abbreviations used throughout are the following: AMNH, American Museum of Natural History (New York); ANSP, Academy of Natural Sciences of Philadelphia; BMNH, The Natural History Museum (London); BYU, Brigham Young University (Provo, Utah); CAS, California Academy of Sciences (San Francisco); FMNH, The Field Museum (Chicago); KU, University of Kansas Museum of Natural History (Lawrence); LACM, Natural History Museum of Los Angeles County (Los Angeles); MCZ, Museum of Comparative Zoology (Cambridge, Massachusetts); MVZ, Museum of Vertebrate Zoology (Berkeley, California); UCR, Universidad de Costa Rica (San José); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); USNM, National Museum of Natural History, Smithsonian Institution (Washington, D.C.).

Bracketed data associated with localities here and elsewhere in the text are inferences derived from sources other than original data associated with specimens as recorded in literature, museum or collectors' catalogues, or specimen labels. The identifications of UCR specimens marked with "(ID)" following the catalogue number were verified by Savage but data are not included in character summaries (e.g., Table 1). A gazetteer, including geographic coordinates of localities, is given in Appendix 2.

Costa Rica: *Alajuela:* Cinchona, 1,600 m, KU 31969, 63788, 63809. Cinco Esquinas [Cantón Alajuela, Distrito Carrizal], 1,700 m, UCR 9039. Grecia [Cantón Grecia, Distrito Grecia], 999 m, UCR 14358. Isla Bonita [Cantón

Alajuela, Distrito Sarapiquí], FMNH 101747–48, 103110; UCR 673 (1,200 m). Poás [1,148 m] (Solórzano, 2004: fig. 57). Poasito [Cantón Alajuela, Distrito Sabanilla], 2,000 m, UCR 18390. Salto El Angel (Río La Paz), LACM 149225. Between Salto La Paz and Cariblanco, 30 km by rd from Puerto Viejo [de Sarapiquí], 850 m, LACM 149215. *Cartago*: Parque Nacional Tapantí, 0.5 km S Puente Río Grande de Orosi y Quebrada Dos Amigos [Cantón Paraiso, Distrito Orosi], 1,650 m, UCR 13746. *Guanacaste*: Cerro Cacao (Köhler, 2003: fig. 477).

Heredia: Refugio Nacional de Vida Silvestre Jaguarundi, Cerro Chompipe, Río Las Vueltas [Cantón Heredia, Distrito Varablanca], 2,000 m, UCR 15500. [Volcán] Barva, Puente Río Segundo [Cantón Barva, Distrito Barva], 1,160 m, UCR 5238 (1D). Zona Protectora La Selva, trail from "1500 m" camp to "2050 m" camp, LACM 149219. *Limón*: Sara (Madre de Dios), MVZ 36450 (questionable record; see Distribution). *Puntarenas*: 5 km W Alturas de Cotón [Cantón Coto Brus, Distrito Sabalito], 1,400 m, UCR 10879. Finca Helechales, 15 km NE Potrero Grande, 1,050 m, LACM 149217. Finca Las Alturas, 1–2 km along trail on N side of Río Cotón, trail to [Finca] Las Tablas, LACM 149214. Finca Las Cruces [=Las Cruces Biological Station] and vicinity, LACM 149216, LACM 149220–21. Finca Las Tablas, pasture at base of Cerro Pando, LACM 149213. Monteverde [Cantón Puntarenas, Distrito Monte Verde], 1,400 m, UCR 1055 (1D). Monteverde Cloud Forest Preserve, near Feinsinger Plot A, LACM 149222. Monteverde Cloud Forest Preserve, near Feinsinger Plot B, LACM 149229. Monteverde Cloud Forest Preserve, about 1,600 m (Savage, 2002: Plate 417; Solórzano, 2004: fig. 58). 1.5 km SE Monteverde, 1,500 m, LACM 149223. Monteverde, near Pensión Flor Mar, LACM 149224. About 20 m before Ovidio Leiton's barn above Campbell's fork, upper Monteverde, LACM 149227.

San José: Cascajal [Cantón Vázquez De Coronado, Distrito Cascajal], UCR 9427 (1,730 m), UCR 14112 (1,770 m), UCR 15501 (1,720 m). Copey, En el camino de Providencia a la Chaqueta, área bosque [Cantón Dota, Distrito Copey], 1,400 m, UCR 16583. Copey, Providencia, Trapiche Quebrada sitio Toma1 a unos 1370 m.s.n.m. [Cantón Dota, Distrito Copey], 1,370 m, UCR 16611. Junction of Río Claro and Río La Hondura, 1,150 m, LACM 149218, 149226. La Candelaria, AMNH 17268 (holotype). Naranjo [Cantón Dota, Distrito Santa Maria], 1,800 m, UCR 3909. Naranjo, Alto Naranjo [Cantón Dota, Distrito Santa Maria], 2,100 m, UCR 3383. Parque Nacional Braulio Carrillo, Tres Marías [Cantón Vázquez De Coronado, Distrito Dulce Nombre de Jesús], 2,047 m, UCR 18821. San Gerardo [Cantón Turrubares, Distrito Carara], 2,360 m, UCR 6256. 14.2 km N San Isidro del General, near Río Payner, 1,500 m, LACM 149228. 13 km N San Isidro del General, 1,420 m, KU 91788.

Panama: *Bocas del Toro*: E slopes Cerro Colorado near continental divide, 1,300–1,600 m, AMNH R-119734. N slope Cerro Pando, 1,450 m, KU 107657–58. Rancho Mojica, BYU 19150 (not seen; Lieb, 1988). *Chiriquí*: Boquete and vicinity, 1,100 m, UMMZ 57909–10 (not seen). Boquete, UMMZ 57973. Vicinity N of Boquete, CAS 78896–900. Quiel, Boquete area, about 1,500 m, MCZ R-34319. Continental divide NE Cerro Colorado, about 1,500 m, AMNH R-119735–36. Western slopes of Cerro Hornito, 1,100 m, AMNH R-124013, R-129754. Mt Copete, 6,900 feet elev. [2,104 m], AMNH R-73326–27. Finca Lérida, Volcán Chiriquí, 5,300 feet [1,615 m], ANSP 22600–01, 22916–18. Fortuna Dam, upper Río Chiriquí, 1,000 m, AMNH R-114315–16. Fortuna, Panama (Köhler, 2008: fig. 578). Pan American Hwy, 10 mi from Costa Rica [=highland road at Finca Santa Clara]; 4,300 ft [1,300 m], AMNH R-73329. Petroterminal pipeline road, Quebrada de Arena, 1,050–1,100 m, AMNH R-124011-12. Continental divide above upper Quebrada de Arena [upper Río Chiriquí drainage], 1,250–1,410 m, AMNH R-129755–56. [Finca] Santa Clara, R. Hartmann's finca NW of Volcán [Chiriquí (Barú)], 4,000 ft. [1,220 m], UMMZ 155733.

APPENDIX 2. GAZETEER AND NOTES ON LOCALITIES

Alturas de Cotón [Cantón Coto Brus, Distrito Sabalito], 5 km W of, 1,400 m. Puntarenas Province, Costa Rica. 08°56′42″N, 82 51′04″W.

Barva. See [Volcán] Barva.

Boquete. Chiriquí Province, Panama. 08 47′N, 82°26′W. A town on the Pacific slope of western Panama near Volcán Barú. Quiel (08 48′N, 82°28′W; 1,830–2,135 m) is an outlying section of the town of Boquete (Blake, 1958: 503).

Cariblanco, 865 m. Alajuela province, Costa Rica. 10°16′08″N, 84°10′53″W.

Cascajal [Cantón Vázquez De Coronado, Distrito Cascajal], 1,720–1,770 m. San José Province, Costa Rica. 10°01′N, 83°57′W.

Cerro Cacao, Guanacaste Province, Costa Rica. 10°56′03″N, 085°27′02″W. Köhler (2003: fig. 477) provided a color illustration of a *Dendrophidion paucicarinatum* from Cerro Cacao.

Cerro Chompipe. See Refugio Nacional de Vida Silvestre Jaguarundi.

Cerro Colorado and Cerro Santiago. E slopes near continental divide, 1,300–1,600 m [approximately 08°32′N, 81°48′W]. Bocas del Toro and Chiriquí provinces, Panama; now in the comarea of Ngäbe-Buglé (see note below). Cerro Colorado is in the Serranía de Tabasará just southwest of the continental divide at approximately 81 48′W (Myers and Duellman, 1982); Cerro Santiago is a short distance to the east. The southeastern-most known localities for *D. paucicarinatum* are in the Cerro Colorado area. Grace Tilger of the AMNH worked in this area for several weeks in 1978–79 (Myers and Duellman, 1982). The localities span the low continental divide, with localities north of the divide formerly in Bocas del Toro Province and those south of the divide formerly in Chiriquí Province. The area is described and illustrated by Myers and Duellman (1982: 2 and fig. 1).

In 1997 portions of the Panamanian provinces of Bocas del Toro, Chiriquí, and Veraguas were combined to form a new administrative unit, comarca of Ngäbe-Buglé. The new political unit encompasses

all cited localities in the Cerro Colorado/Cerro Santiago region and Atlantic versant localities (formerly Bocas del Toro province) in the Cerro Fortuna area.

Cerro Copete or Mt. Copete (also called La Campana; or simply Copete) [08°48′45″N, 82°31′15″W]. Chiriquí Province, Panama. One of the foothills east of the summit of Volcán de Chiriquí (Barú) and west of Finca Lérida. Peak elevation about 3,050 m. See Blake (1958: foldout map between pp. 502–503).

Cerro Fortuna. See Fortuna Dam.

Cerro Hornito, western slopes of, 1,100 m. Chiriquí Province, Panama. 08°39′N, 82°11″W.

Cerro Pando, north (Atlantic) slope, 1,450 m. Bocas del Toro Province, Panama. 09°00′N, 82°41′W. For KU 107657–58, the route itinerary and physiognomy of the forest are described by Myers (1969: 33–36) and Trueb (1968). Some of their descriptive comments are quoted in the text (Natural History of *Dendrophidion paucicarinatum*). The elevation of the collection locality for KU 107657–58 given here, 1,450 m (Appendix 1), is taken from field notes of Charles W. Myers, who collected the specimens; KU electronic databases recorded the elevation as 1,300 m as of 2012.

Cerro Santiago. See Cerro Colorado.

Cinchona. See Isla Bonita.

Cinco Esquinas [Cantón Alajuela, Distrito Carrizal], 1700 m, Alajuela province, Costa Rica. 10°06′10″N, 84°10′W.

Copete. See Cerro Copete.

Copey, En el camino de Providencia a la Chaqueta, área bosque [Cantón Dota, Distrito Copey], San José province, Costa Rica. 1,400 m. 09°32′07″N, 83°51′30″W.

Copey, Providencia, Trapiche Quebrada sitio Toma1, 1,370 m elevation [Cantón Dota, Distrito Copey]. San José Province, Costa Rica. 09°31′29″N, 83°52′48″W.

Finca El Helecho. See Finca Helechales.

Finca Helechales, 15 km NE Potrero Grande, 1,050 m [09°04′N, 83°05′W], Puntarenas Province, Costa Rica. This locality is recorded as "Finca El Helecho" in some databases and online sources but that orthography seems to be an error. The relevant specimen cited here, LACM 149217 (formerly CRE 8271), was collected by Roy W. McDiarmid, who recorded the locality in field notes as "Finca El Helechales". The site is on the Sabanas Helechales and appears on the Costa Rican topo sheet 3543 II Cabagra as "Finca Helechales". The finca was later sold to be developed as a tourist lodge but was confiscated by the Costa Rican government in the 1990s to be integrated into Amistad National Park.

Finca Las Alturas, 1,330 m. Puntarenas Province, Costa Rica. 08°57′N, 82°50′W. Presently the Las Alturas Biological Station operated by the Organization for Tropical Studies.

Finca Las Cruces (or "Las Cruces"). Puntarenas Province, Costa Rica. About 4 km S San Vito, 1,200 m. 08°47′35″N, 82°57′30″W. Presently the

Las Cruces Biological Station operated by the Organization for Tropical Studies.

Finca Las Tablas, pasture at base of Cerro Pando, Puntarenas Province, Costa Rica. 08°57′N, 82°44′W.

Finca Lérida, Volcán de Chiriquí, 5,300 feet [1,615 m;]. Chiriquí Province, Panama. 8°49′N, 82°34′W. The name given generally to the former coffee plantation of the Mönniche family on the eastern slopes of Volcán Chiriquí, and used extensively by biologists from the 1930s to the 1950s. About 4.5 miles W and NW of the town of Boquete (Blake, 1958: 503 and foldout map). Dunn (1947) reported on snakes from Finca Lérida collected over a period of about 7 years, mainly in connection with the Panamanian Snake Census. 5,000–7,400 ft. [1,500–2,150 m].

Finca Santa Clara. See Santa Clara.

Fortuna Dam. Chiriquí Province, Panama. Fortuna Dam is on the upper Río Chiriquí, 1,000 m. 08°44′N, 82°17′W. Köhler (2008: fig. 578) portrayed in color a specimen of *D. paucicarinatum* from "Fortuna". A cloud forest reserve, the Reserva Forestal de Fortuna, is also in this area. Myers and Duellman (1982: 12 and following) discussed the geography of this area and their comments are quoted extensively in the section herein on natural history. These authors considered the Cerro Fortuna area to arbitrarily delimit the eastern end of the Cordillera de Talamanca and beginning of the Serranía de Tabasará. See also Savage and Myers (2002: 6–7 and fig. 2).

Grecia [Cantón Grecia, Distrito Grecia], 999 m, Alajuela province, Costa Rica. 10°04′30″N, 84°18′46″W. On the lower slopes of Volcán Poás at about 3,500 feet [1,070 m] (Carriker, 1910: 342).

Isla Bonita and Cinchona, Alajuela province, Costa Rica. 10°01′N, 84°01′W. On the eastern slope of Volcán Poás. The region is mapped in Savage (1974: fig. 1). According to Savage (1974: 79) "The entire area [from near] Varablanca (1,804 m) north to Cariblanco (830 m) was called Cinchona or Isla Bonita by Edward H. Taylor [e.g., Taylor, 1954], ... Isla Bonita lies at the northern end of the cinchona plantation at 1,200-m elevation. In addition to the areas sampled by Taylor, other important landmarks from south to north along the road are the Río La Paz Grande and its beautiful waterfall, Salto El Angel, at 1,380 m, Río La Paz Pequeño (1,370 m) and the Río Santiaguito area and stone quarry (1,350 m) 0.6 km south of Cinchona... it is apparent that Taylor's published localities and elevations are somewhat confused and inconsistent ... Most of these places are in Provincia de Alajuela and not Heredia as often reported." Premontane Pluvial bioclimate in the Holdridge system (Holdridge, 1967).

La Candelaria. San José Province, Costa Rica. 09°47′17″N, 84°07′24″W; ca. 1,170 m fide Google-Earth. The type locality of *D. paucicarinatum*. See discussion of type locality in the text. Also known as Monte Redondo.

Lérida. See Finca Lérida.

La Selva. See Zona Protectora.

Las Alturas. See Finca Las Alturas.

Las Cruces. See Finca Las Cruces.

Monte Redondo. See La Candelaria.

Monteverde [Cantón Puntarenas, Distrito Monte Verde], Puntarenas Province, Costa Rica. 1,400 m. Monteverde refers to several locales in northern Puntarenas Province, including a village of that name (10 18′N, 84 49′W; 1,360 m) and the Monteverde Cloud Forest Reserve (10 19′N, 84 47′W; about 1,500–1,860 m). The herpetofauna is discussed in Pounds (2000) and checklists of the herpetofauna are given by Hayes et al. (1989) and Pounds and Fogden (2000). The geography, climate, and forest types are covered in Clark et al. (2000).

Naranjo [Cantón Dota, Distrito Santa Maria], 1,800 m; Alto Naranjo [Cantón Dota, Distrito Santa Maria], 2,100 m; and Santa Maria Dota, south of Naranjo. San José Province, Costa Rica. 09 36′N, 83 57′W. Santa Maria de Dota is in the upper drainage of the Río Pirrís (Savage, 1974: 108). Goodwin (1946: 457) stated that Naranjo was a village on the Río Parrito about 12 miles S of Cartago. Carriker (1910: 341) stated that Santa Maria de Dota "is heavily wooded, has a cool climate with a heavy rainfall…"

Pan American Hwy, 10 mi from Costa Rica. See Santa Clara.

Parque Nacional Braulio Carrillo, Tres Marías [Cantón Vázquez De Coronado, Distrito Dulce Nombre de Jesús], 2,047 m, San José Province, Costa Rica. 10 04′05″N, 84 01′W (coordinates from UCR).

Parque Nacional Tapantí, 0.5 km S Puente Río Grande de Orosi y Quebrada Dos Amigos [Cantón Paraiso, Distrito Orosi], 1,650 m. Cartago Province, Costa Rica. 09 41′48″N, 83 47′W.

Poasito [Cantón Alajuela, Distrito Sabanilla], 2,000 m, Alajuela Province, Costa Rica. 10 10′06″N, 84 11′48″W. On the headwaters of the Río Poás (Savage, 1974: 102 and fig. 1 [map]).

Quebrada de Arena and Petroterminal pipeline road, Chiriquí Province, Panama. 08°46′32″N, 82 12′43″W (Myers and Duellman, 1982: 32). Charles W. Myers and associates worked in this area (1,050–1,410 m), which is about 0.6 km SW of the continental divide in the upper Río Chiriquí drainage and along a road running from Puerto Armuelles on the Pacific versant to Chiriquí Grande on the Atlantic coast (Myers and Duellman, 1982: 29, 32 and fig. 24). Cloud forest is or was present on a low section of the continental divide (approximately longitude 82 12′31″W) at about 1,120 m (Myers et al., 1984: footnote 4). Descriptions of the environment are given by Myers and Duellman (1982) and Myers et al (1984: 13 and fig. 8), both quoted in the text (Natural History of *Dendrophidion paucicarinatum*).

Quiel. See Boquete.

Rancho Mojica. Bocas del Toro Province, Panama. Near 09 02′N, 82 41″W. Near the Río Changena, 4,800–5,600 ft. [1,463–1,707 m] (Fairchild and Handley, 1966).

Refugio Nacional de Vida Silvestre Jaguarundi, Cerro Chompipe, Río Las Vueltas [Cantón Heredia, Distrito Varablanca], 2,000 m. Heredia Province, Costa Rica. 10 05′46″N, 84 04′W.

Río Claro and Río La Hondura, junction of, 1,150 m. San José Province, Costa Rica. 10 04′24″N, 83 58′. Premontane Pluvial bioclimate. See Savage, 1974: 92–93 and fig. 2.

Río de la Paz. See Salto El Angel.

Salto El Angel (Río La Paz Grande) [= Salto La Paz Grande or Salto La Paz], Alajuela Province, Costa Rica. Approximately 10 12′N, 84 09′30″W (from Costa Rica topo sheet 3346 I Poás). At 1,380 m fide Savage (1974: 76 and fig. 1 [map]) but GoogleEarth places it at about 1,560 m. This locality, properly called Salto La Paz Grande or Salto La Paz, has been subject to confusion because the "true" Salto El Angel (Salto del Angel) on the Río Angel is very nearby. In the early years of working in Costa Rica, Savage and colleagues were informed that the waterfall at the Rio La Paz Grande on the main road from the Meseta to the Sarapiquí region was called Salto El Angel, as it has been referred to for many specimens collected at the site. More recently it has been called Salto La Paz Grande or Salto La Paz. The "true" Salto El Angel (Salto del Angel) is off the main road (on the Rio Angel) farther north but we are not aware of anyone who has collected there.

[Between] Salto La Paz and Cariblanco [10 16′08″N, 84°10′53″W], 30 km by road from Puerto Viejo, 850 m [10 14′42″N, 84 10′16″W]. Heredia Province, Costa Rica. See comments on waterfall names under Salto El Angel.

San Gerardo [Cantón Turrubares, Distrito Carara], 2,360 m, San José province, Costa Rica. 09 33′N, 83 49′W.

San Isidro del General, (14.2 km N of, nr. Río Payner. 1,500 m; 13 km N of, 1,420 m). San José Province, Costa Rica. Approximately 09 29′38″N, 83 42′W. On the western slope of the Sierra de Talamanca.

Santa Clara, R. Hartmann's finca NW of Volcán [Chiriquí (Barú)], 4,000 ft. [1,220 m]; and Pan American Hwy, 10 mi from Costa Rica [=highland road at Finca Santa Clara]; 4,300 ft [1,300 m]. Chiriquí Province, Panama. 08 50′N, 82 46′W. See also Fairchild and Handley (1966).

Santa Maria Dota. See Naranjo.

Sara (Madre de Dios) [40 m]. Limón Province, Costa Rica. 10 08′10″N, 83 21′21″W. A questionable lowland locality for *D. paucicarinatum*. See Distribution and Fig. 7.

[Volcán] Barva, Puente Río Segundo [Cantón Barva, Distrito Barva], 1,160 m. Heredia Province, Costa Rica. 10 01′N, 84 07′30″W (coordinates from UCR database entry for UCR 5238).

Volcán Barú (=Volcán de Chiriquí). Chiriquí Province, Panama. 08 48′N, 82 32′30″W.

Zona Protectora La Selva, trail from "1,500 m" camp to "2,050 m" camp. Heredia Province, Costa Rica. Approximately 10 25′N, 84 01′W. The specimen of *D. paucicarinatum* from this locality was part of a

biological survey of the protected area now connecting La Selva with Braulio Carrillo National Park. See Pringle et al. (1984).

LITERATURE CITED

AMARAL, A. D. "1929" [1930]. Estudos sobre ophidios neotropicos. XVIII—lista remissiva dos ophidios da Região Neotropica. *Memorias do Instituto Butantan* **4**: 127–128, 129–271.

AUTH, D. L. 1994. Checklist and bibliography of the amphibians and reptiles of Panama. *Smithsonian Herpetological Information Service* **98**: 1–59.

BLAKE, E. R. 1958. Birds of Volcán de Chiriquí, Panama. *Fieldiana, Zoology* **36**: 499–577, foldout map.

BOLAÑOS, F., J. M. SAVAGE, AND G. CHÁVES. 2010. Anfibios y reptiles de Costa Rica (versión: 18 de Agosto del 2010), pp. 1–19. *In Listas Zoológicas Actualizadas UCR.* San Pedro: Museo de Zoología, Universidad de Costa Rica. [Modified 18 August 2010; accessed 2 February 2013]. Available from: http://museo.biologia. ucr.ac.cr.

BOULENGER, G. A. 1896. *Catalogue of the Snakes in the British Museum (Natural History).* Vol. III. London: British Museum (Natural History).

CADLE, J. E. 2010. Systematics, natural history, and hemipenial morphology of *Dendrophidion brunneum* (Günther), a poorly known snake from the Andes of Ecuador and Peru. *Zootaxa* **2433**: 1–24.

CADLE, J. E. 2012a. Cryptic species within the *Dendrophidion vinitor* complex in Middle America (Serpentes: Colubridae). *Bulletin of the Museum of Comparative Zoology* **160**: 183–240.

CADLE, J. E. 2012b. Systematics of the Neotropical snake *Dendrophidion percarinatum* (Serpentes: Colubridae), with descriptions of two new species from western Colombia and Ecuador and supplementary data on *D. brunneum. Bulletin of the Museum of Comparative Zoology* **160**: 259–344.

CADLE, J. E., AND J. M. SAVAGE. 2012. Systematics of the *Dendrophidion nuchale* complex (Serpentes: Colubridae) with the description of a new species from Central America. *Zootaxa* **3513**: 1–50.

CARRIKER, M. A., JR. 1910. An annotated list of the birds of Costa Rica including Cocos Island. *Annals of the Carnegie Museum of Natural History* **6**: 314–970.

CLARK, K. L., R. O. LAWTON, AND P. R. BUTLER. 2000. The physical environment, pp. 15–38. *In* N. M. Nadkarni and N. T. Wheelwright (eds.), *Monteverde: Ecology and Conservation of a Tropical Cloud Forest.* New York: Oxford University Press.

COPE, E. D. 1894. Third addition to a knowledge of the batrachia and reptilia of Costa Rica. *Proceedings of the Academy of Natural Sciences of Philadelphia* **46**: 194–206.

COPE, E. D. "1894" [1895]. On a collection of Batrachia and Reptilia from the island of Hainan. *Proceedings of the Academy of Natural Sciences of Philadelphia* **46**: 423–428.

COPE, E. D. 1895. The classification of the Ophidia. *Transactions of the American Philosophical Society* **18**: 186–219, pls. 14–33.

DUNN, E. R. 1947. Snakes of the Lérida Farm (Chiriquí Volcano, western Panamá). *Copeia* **1947**: 153–157.

FAIRCHILD, G. B., AND C. O. HANDLEY, JR. 1966. Gazetteer of collecting localities in Panama, pp. 9–20, map. *In* R. L. Wenzel and V. J. Tipton (eds.), *Ectoparasites of Panama.* Chicago: Field Museum of Natural History.

FREIRE, E. M. J., U. CARAMASCHI, AND U. GONÇALVES. 2010. A new species of *Dendrophidion* (Serpentes: Colubridae) from the Atlantic rain forest of northeastern Brazil. *Zootaxa* **2719**: 62–68.

GOLDBERG, S. R. 2003. Reproduction in four species of *Dendrophidion* from Costa Rica (Serpentes: Colubridae). *Transactions of the Illinois State Academy of Science* **96**: 295–300.

GOODWIN, G. G. 1946. Mammals of Costa Rica. *Bulletin of the American Museum of Natural History* **87**: 271–474, pl. 17.

HAYES, M. P., J. A. POUNDS, AND W. W. TIMMERMAN. 1989. *An Annotated List and Guide to the Amphibians and Reptiles of Monteverde, Costa Rica.* Tyler, Texas: Society for the Study of Amphibians and Reptiles.

HOLDRIDGE, L. R. 1967. *Life Zone Ecology.* Revised edition. San José, Costa Rica: Tropical Science Center.

IBÁÑEZ D. R., AND F. A. SOLÍS. "1991" [1993]. Las serpientes de Panamá: lista de especies, comentarios taxonómicos y bibliografia. *Scientia (Panamá)* **6**: 27–52.

KLAUBER, L. M. 1943. Tail-length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. *Bulletins of the Zoological Society of San Diego* **18**: 1–60.

KÖHLER, G. 2003. *Reptiles of Central America.* English edition. Offenbach, Germany: Herpeton.

KÖHLER, G. 2008. *Reptiles of Central America.* 2nd English edition. Offenbach, Germany: Herpeton.

LAYNE, J. N., AND T. M. STEINER. 1984. Sexual dimorphism in occurrence of keeled dorsal scales in the eastern indigo snake (*Drymarchon corais couperi*). *Copeia* **1984**: 776–778.

LIEB, C. S. 1988. Systematic status of the Neotropical snakes *Dendrophidion dendrophis* and *D. nuchalis* (Colubridae). *Herpetologica* **44**: 162–175.

LIEB, C. S. 1991. *Dendrophidion paucicarinatum. Catalogue of American Amphibians and Reptiles* **521**: 521.1–521.2.

MYERS, C. W. 1969. The ecological geography of cloud forest in Panama. *American Museum Novitates* **2396**: 1–52.

MYERS, C. W. 1982. Blunt-headed vine snakes (*Imantodes*) in Panama, including a new species and other revisionary notes. *American Museum Novitates* **2738**: 1–50.

MYERS, C. W. 2003. Rare snakes—five new species from eastern Panama: reviews of northern *Atractus* and

southern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates* 3391: 1–47.

MYERS, C. W., AND J. E. CADLE. 1994. A new genus for South American snakes related to *Rhadinaea obtusa* Cope (Colubridae) and resurrection of *Taeniophallus* Cope for the "*Rhadinaea brevirostris*" group. *American Museum Novitates* 3102: 1–33.

MYERS, C. W., AND J. E. CADLE. 2003. On the snake hemipenis, with notes on *Psomophis* and techniques of eversion: a response to Dowling. *Herpetological Review* 34: 295–302.

MYERS, C. W., J. W. DALY, AND V. MARTINEZ. 1984. An arboreal poison frog (*Dendrobates*) from western Panama. *American Museum Novitates* 2783: 1–20.

MYERS, C. W., AND W. E. DUELLMAN. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates* 2752: 1–32.

NATIONAL GEOSPATIAL-INTELLIGENCE AGENCY (NGA) [INTERNET]. Springfield, Virginia: NGA GEOnet Names Server (GNS) (US). Available from GeoNames Search at http://geonames.nga.mil. Accessed January–February 2013.

PÉREZ-SANTOS, C. 1999. *Serpientes de Panamá/Snakes of Panama*. Seville: Comité Español del Programa MaB y de la Red IberoMaB de la UNESCO.

PÉREZ-SANTOS, C., A. G. MORENO, AND A. GEARHART. 1993. Checklist of the snakes of Panama. *Revista Española de Herpetología* 7: 113–122.

PETERS, J. A., AND B. OREJAS-MIRANDA. 1970. Catalogue of the Neotropical Squamata: Part I. Snakes. *Bulletin of the United States National Museum* 297: 1–347.

POUNDS, J. A. 2000. Amphibians and reptiles, pp. 149–177. *In* N. M. Nadkarni and N. T. Wheelwright (eds.), *Monteverde, Ecology and Conservation of a Tropical Cloud Forest*. New York: Oxford University Press.

POUNDS, J. A., AND M. P. L. FOGDEN. 2000. Amphibians and reptiles of Monteverde, pp. 537–540. *In* N. M. Nadkarni and N. T. Wheelwright (eds.), *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York.

POUNDS, J. A., M. P. L. FOGDEN, J. M. SAVAGE, AND G. C. GORMAN. 1997. Tests of null models for amphibian declines on a tropical mountain. *Conservation Biology* 11: 1307–1322.

PRINGLE, C. M., I. CHACON, M. GRAYUM, H. W. GREENE, G. HARTSHORN, G. SCHATZ, G. STILES, C. GOMEZ, AND M. RODRIGUEZ. 1984. Natural history observations and ecological evaluation of the La Selva Protection Zone, Costa Rica. *Brenesia* 22: 189–206.

PRUDENTE, A. L. C., G. F. MASCHIO, C. E. YAMASHINA, AND M. C. SANTOS-COSTA. 2007. Morphology, reproductive biology and diet of *Dendrophidion dendrophis* (Schlegel, 1837) (Serpentes, Colubridae) in Brazilian Amazon. *South American Journal of Herpetology* 2: 53–58.

SANTOS-BARRERA, G., J. PACHECO, F. MENDOZA-QUIJANO, F. BOLAÑOS, G. CHÁVES, G. C. DAILY, P. R. EHRLICH, AND G. CEBALLOS. 2008. Diversity, natural history and conservation of amphibians and reptiles from the San Vito region, southwestern Costa Rica. *Revista de Biología Tropical* 56: 755–778.

SAVAGE, J. M. 1973. *A Preliminary Handlist of the Herpetofauna of Costa Rica*. Lawrence, Kansas: American Society of Ichthyologists and Herpetologists.

SAVAGE, J. M. 1974. Type localities for species of amphibians and reptiles described from Costa Rica. *Revista de Biología Tropical* 22: 71–122.

SAVAGE, J. M. 1980. *A Handlist with Preliminary Keys to the Herpetofauna of Costa Rica*. Los Angeles: Allan Hancock Foundation.

SAVAGE, J. M. 2002. *The Amphibians and Reptiles of Costa Rica, a Herpetofauna between Two Continents, between Two Seas*. Chicago: The University of Chicago Press.

SAVAGE, J. M., AND F. BOLAÑOS. 2009. A checklist of the amphibians and reptiles of Costa Rica: additions and nomenclatural revisions. *Zootaxa* 2005: 1–23.

SAVAGE, J. M., AND C. W. MYERS. 2002. Frogs of the *Eleutherodactylus biporcatus* group (Leptodactylidae) of Central America and northern South America, including rediscovered, resurrected, and new taxa. *American Museum Novitates* 3357: 1–48.

SAVAGE, J. M., AND J. VILLA. 1986. *Introduction to the Herpetofauna of Costa Rica/Introducción a la Herpetofauna de Costa Rica*. Ithaca, New York: Society for the Study of Amphibians and Reptiles.

SCOTT, N. J., JR. 1976. The abundance and diversity of the herpetofaunas of tropical forest litters. *Biotropica* 8: 41–58.

SCOTT, N. J., JR., J. M. SAVAGE, AND D. C. ROBINSON. 1983. Checklist of reptiles and amphibians, pp. 367–374. *In* D. H. Janzen (ed.), *Costa Rican Natural History*. Chicago: University of Chicago Press.

SHINE, R. 1993. Sexual dimorphism in snakes, pp. 49–86. *In* R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Behavior*. New York: McGraw Hill, Inc.

SHINE, R. 1994. Sexual size dimorphism in snakes revisited. *Copeia* 1994: 326–346.

SLEVIN, J. R. 1942. Notes on a collection of reptiles from Boquete, Panama, with the description of a new species of *Hydromorphus*. *Proceedings of the California Academy of Sciences* 23: 463–480.

SMITH, H. M. 1941. A new name for the Mexican snakes of the genus *Dendrophidion*. *Proceedings of the Biological Society of Washington* 54: 73–76.

SMITH, H. M. 1958. Handlist of the snakes of Panama. *Herpetologica* 11: 222–224.

SOLORZANO, A. 2004. *Serpientes de Costa Rica: Distribución, Taxonomía e Historia Natural/Snakes of Costa Rica: Distribution, Taxonomy and Natural History*. Eagle Mountain, Utah: Eagle Mountain Publishing, LC.

STAFFORD, P. J. 2003. Trophic ecology and reproduction in three species of Neotropical forest racer

(*Dendrophidion*; Colubridae). *Herpetological Journal* **13:** 101–111.

STUART, L. C. 1933. Studies on Neotropical Colubrinae: III. The taxonomic status of certain Neotropical racers. *Copeia* **1933:** 9–10.

TAYLOR, E. H. 1951. A brief review of the snakes of Costa Rica. *University of Kansas Science Bulletin* **34, part 1:** 3–188.

TAYLOR, E. H. 1954. Further studies on the serpents of Costa Rica. *University of Kansas Science Bulletin* **36, part 2:** 673–801.

TRUEB, L. 1968. Variation in the tree frog *Hyla lancasteri. Copeia* **1968:** 285–299.

VILLA, J., L. D. WILSON, AND J. D. JOHNSON. 1988. *Middle American Herpetology—A Bibliographic Checklist.* Columbia: University of Missouri Press.

Photo on the front cover:

Hemipenis of *Dendrophidion paucicarinatum* shown in sulcate and asulcate views. The organ has been fully everted and inflated with colored petroleum jelly.